# Taxonomy of Tropical West African Bivalves IV. Arcidae

by P. Graham OLIVER and Rudo VON COSEL

Abstract. - Twenty species of Arcidae are described from tropical West Africa, defined here as between 23° N and 17° S. The Arcinae are represented by four genera and include four new taxa : Arca avellana turbatrix n. subsp., Barbatia gabonensis n. sp., B. ionthados n. sp., B. (Nipponarca) allocostata n. sp. The anatomy of the latter is described and confirms the value of the subgenus which is redefined. The Anadarinae, other than Senilia and Bathyarca are all included in the genus Anadara because the use of the ligament orientation and inequivalve condition are abandoned as phyletic characters. Two new species are described : Anadara eborensis n. sp. and A. camerunensis n. sp. A. polii (Mayer) is the species often cited as "A. diluvii (Lamarck)" in publications concerning the Mediterranean. Variation within species is frequent, notably in Anadara polii and A. senegalensis. Ecological factors and geographical clines are invoked to explain some of this variation but local genetic isolation could not be excluded. The relationships of the shallow water West African species are analysed and compared to the faunas of the Mediterranean, Caribbean, Panamic and Indo-Pacific regions. Only one genus is endemic to West Africa, namely Senilia. There are three species common to the Mediterranean but none to the Caribbean although there are sibling species. Overall similarity is greatest with the Indo-Pacific but the Anadarinae in isolation have affinity to the Panamic fauna. A general discussion on the zoogeographical patterns for all the Arcoidea is presented in the concluding part of this study which is to be published in the next issue of the Bulletin du Muséum.

Résumé. — Description de vingt espèces d'Afrique occidentale tropicale, ici définie entre 23°N et 17°S. Les Arcinae sont représentés par quatre genres; quatre taxa nouveaux y sont inclus : Arca avellana turbatrix n. subsp., Barbatia gabonensis n. sp., B. ionthados n. sp., B. (Nipponarca) allocostata n. sp. L'anatomie de la dernière est décrite, confirmant la valeur du sous-genre ici redéfini. Outre Senilia et Bathyarca, toutes les Anadarinae sont incluses dans le genre Anadara, car l'utilisation de l'orientation du ligament et l'inégalité des deux valves sont abandonnées en tant que caractères phylétiques. Deux espèces nouvelles, Anadara eborensis n. sp. et A. camerunensis n. sp. sont décrites. Dans des publications concernant la Méditerranée, A. polii (Mayer) a été souvent citée comme « A. diluvii (Lamarck) ». Une variabilité intraspécifique est fréquente, surtout chez A. polii et A. senegalensis. Des facteurs écologiques ainsi que des clines géographiques sont évoqués pour l'explication d'une partie de cette variabilité, mais on ne peut pas exclure d'une isolation génétique locale. Les espèces du plateau continental ouest-africain sont analysées sur le plan de leurs relations, et comparées avec les faunes de la Méditerranée, des Caraïbes, du Pacifique panaméen et de l'Indo-Pacifique. Senilia est l'unique genre d'Arcidae endémique de l'Afrique occidentale. Trois espèces vivent aussi en Méditerranée, mais aucune n'est présente dans les Caraïbes bien qu'il y ait des espèces jumelles. Les Arcidae dans leur ensemble présentent le maximum de similitude avec celles de l'Indo-Pacifique; cependant les Anadarinae montrent une affinité plus marquée avec celles du Pacifique panaméen. Une discussion générale sur la répartition zoogéographique de tous les Arcoidea se trouve dans une deuxième partie de cette étude, qui sera publiée dans le prochain numéro du Bulletin du Muséum.

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#### INTRODUCTION

This paper on the Arcidae and the forthcoming second part on the Noetiidae (which also will contain the concluding discussion) are parts of a revision of the Bivalvia of tropical West Africa being undertaken by the second author and made possible by the availability of recent collections through ORSTOM (with main part of the fieldwork by the second author) and Serge GOFAS (MNHN). The region is defined here as lying between Rio de Oro (southern part of West Sahara, 23° N) and Baia dos Tigres (Southern Angola, 17° S). Previous studies of the region are sparse with only the work of DAUTZENBERG (1909, 1913, 1927) and NICKLÈS (1950, 1955) of note. These papers illustrate the concept of shared taxa with the Caribbean and Mediterranean regions but the recognition of pan Atlantic species and local species appears to be inconsistent. For example the Barbatia candida/complanata complex was usually considered to be a single pan Atlantic species but the equally confusing Arcopsis afra/adamsi complex (cf. second part, OLIVER and COSEL, in print) has always been regarded as two distinct species. Interestingly A. afra has also been widely cited from the Indo-Pacific. The actual relationships of such apparent circumtropical species complexes have never been elucidated. The aim of this review is therefore twofold : (1) To describe and illustrate all species of Arcoidea from tropical West Africa and (2) To examine the relationships of the west African species to those from the Caribbean. Mediterranean and Indo-Pacific.

In both parts, data on the morphometrics of the shells are frequently presented as box plots. The box represents the range of values of the first thirty percent of the sample either side of the mode, the projecting lines the next ten percent and the outlying points the remainder of the values. We have used these as we feel they give a rapid visual understanding of the range of values and the consequent variation. The box plots and all other descriptive and comparative statistics are derived from analyses using Statview SE<sup>TM</sup>.

The general discussion on zoogeographical patterns is presented in the second and concluding part of this paper which will be published in the following issue of this Bulletin.

## Abbreviations used in the text

BMNH : British Museum (Natural History) (now : The Natural History Museum), London, U.K. MNHN : Muséum national d'Histoire naturelle, Paris, France. NMWZ : National Museum of Wales, Dept. of Zoology, Cardiff, U.K. SMF : Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt/M., Germany.

USNM : United States National Museum, Smithsonian Institution, Washington, D.C., USA.

ZMB : Zoologisches Museum der Humboldt-Universität Berlin, Berlin, Germany.

ZMC : Universitets Zoologisk Museum, Copenhagen, Denmark.

leg. : legit, collected by; sh. : shell, shells; spm. : specimen, specimens; sta. : sampling station; v. : valve; RV : right valve; LV : left valve.

## Family ARCIDAE

## Subfamily ARCINAE

## Genus ARCA Linné, 1758

TYPE SPECIES : Arca noae Linné, 1758 (SD Schmidt, 1818, ICZN Opinion 189).

## Arca noae Linné, 1758 (Pl. I, 1A-1D, 2; fig. 1; map 1)

Arca noae Linné, 1758 : 693. Arca despecta P. Fischer, 1876 : 258-259; pl. 8, fig. 1.

TYPE MATERIAL : One marked specimen in the Linnean Collection in London (DODGE, 1952 : 143). The holotype of *Arca despecta* Fischer is in MNHN.

TYPE LOCALITY : "M. rubro, Mediterraneo, Indico" but now taken to be the Mediterranean. For A. despecta Fischer "littora Africae occidentalis" but the precise locality is not recorded.

#### DESCRIPTION

Shell to 90 mm in length. Equivalve. Inflated. Inequilateral, beaks in the anterior quarter. Outline narrowly elongate, subtrapezoidal. Posterior area long and narrow usually slightly sulcate; posterior angle initially carinate, becoming rounded but remaining distinct; posterior margin sloping outwards, usually auriculate, may be subtruncate. Median sinus distinct in early stages but becoming obscure; ventral margin straight or sinuous usually indented at byssal gape. Anterior margin sloping inwards, more or less straight or gently curved. Dorsal margin very long, straight.

Dorsal area very long and may be extremely wide, more or less flat; umbonal separation great, umbos low. Ligament initially restricted to a triangular area between the beaks but developing to fill most of the dorsal area. Chevrons initially symmetrical but becoming irregular with numerous insertion sites.

Hinge plate very narrow; teeth in two series, separation obscure but just behind the line of the beaks. Anterior set up to 40 teeth, posterior set up to 60 teeth. Teeth minutely serrated, more or less straight and vertical.

Sculpture primarily radial of narrow ribs, riblets and raised threads. In juveniles there are 30-35 more or less uniform riblets. In adults posterior area with 2-3 subobsolete ribs; posterior angle becoming smooth; postero-median zone with 5-8 narrow ribs which are not much stronger than the 10-15 median riblets; anterior area with 4-6 riblets; all median and anterior zones with interspace raised threads.

Periostracum usually worn remaining around byssal gape and margins, composed of

fragile semidiaphanous straw coloured concentric lamellae with very weak radial thickenings; carinal bristles broad, irregular, laminar, rarely persistent.

External background colour cream to white overlain with closely spaced buff to rust brown oblique somewhat zigzag bands.

Adductor scars unequal, the posterior about twice the size of the anterior. Byssus retractor elongate, triangular, extending along three quarters of the posterior hinge plate.

SELECTED SHELL MEASUREMENTS : For ratios of length to height, length to tumidity and length to anterior to beak length, see figure 3 under Arca bouvieri.

DISTRIBUTION : Eastern Atlantic from southern Portugal (Lagos, Algarve (rare)) south to Senegal M'Bour, 14° N); Canary Islands, Cape Verde Islands; throughout the Mediterranean.

MATERIAL EXAMINED : Mediterranean Morocco : M'diq, on beach, 2 v., leg. GOFAS : Ceuta, Ensenada de la Almadraba, 20-26 m, 1 juv. v., leg. BOUCHET; south of Ceuta, 35°53' N/05°19' W, 50 m, 1 juv. v., leg. VON COSEL, both V. 1986; Melilla, 1 sh., 2 v., coll. Staadt, all MNHN. Algeria : Beni Saf, 1 spm.; Oran, 6 spm., both coll. LOCARD, 1892; 3 sh., 1 v., coll. PALLARY, 1904; 3 v., old coll.; Alger, 1 sh., 2 v., old coll.; all MNHN. Tunisia : Sfax, 2 v., coll. LOCARD, 1892; NW of Bou Grara Sea, Gulf of Gabes, 1 spm., some juv. v.; Borj Djillidj, Djerba Island, 10 spm., Djerba, north coast, on beach, many v.; Canal d'Ajim, Djerba, 10-32 m, many spm., all leg. BOUCHET & WAREN, 1982; all MNHN. Greece : Euboea Channel, 1 spm., coll. Chaper, MNHN. Italy : Venice, 1 sh., coll. MONTEROSATO, 1906; Palerme, 1 sh., coll. ALLERY, 1872; Naples, 3 spm., coll. LOCARD, 1892; 2 sh., coll. PETIT, 1873; all MNHN. Mediterranean France : Cannes, Alpes-Maritimes, 1 spm., 2 sh., old coll. MNHN; St. Tropez, Var, 3 sh.; Porquerolles, Var, 1 sh.; Sanary-sur-Mer, Var, 1 sh.; Marseille, 3 sh.; St. Henri, Bouches-du-Rhône. 1 sh., all coll. LOCARD, 1892, MNHN. Corsica : St. Florent, 1 spm.; Bastia, 1 spm., both coll. LOCARD, 1892; Propriano, on beach, 1 v., leg. DELAUNAY; Ajaccio, 2 spm., coll. LOCARD, 1882; all MNHN. Balearic Islands : Mahon, Menorca, 5 spm., MELVILL-TOMLIN colln., NMWZ. Palma de Mallorca, 12 v., coll. Soyer, 1969, MNHN. Mediterranean Spain : Cadaques, Costa Brava, 3 sh., 1 v., leg. CHERRIERE, 29. VIII. 1966; 5 spm., both old coll. MNHN. Atlantic Morocco : Tanger, 1 spm., 1 sh., coll. PALLARY, MNHN. Canary Islands : Las Palmas, Playa Alcaravaneras, 1 sh., 3 v., in the nets of fishermen; Playa Las Canteras, 5 v., both leg. von CoseL, 1965, MNHN ex coll. von CoseL. West Sahara : off Cap Barbas, 21°05' N/17°14' W, 43-45 m, 2 spm., 1 v., "Calypso"-Sta. 1, leg. MARCHE-MARCHAD, MNHN. Maurita-nia : Port-Étienne (now Nouadhibou), 2 spm., 2 sh., Mission GRUVEL; Pointe des Maures (20°55' N), intertidal, 1 spm., leg. BOUCHET, V.1983; Pointe Cansado, 2 v., Mission GRUVEL, 5.IV.1908; all MNHN. Cape Verde Islands : (without precise locality) 1 v., coll. DE CESSAC, 1877; Santo Antão, Punta do Sal, 5 v., leg. CADENAT; São Vicente, Baia Matiota, Mindelo, 3 m, 3 juv. v., leg. von Cosel, 16.XII.1978; Razo, on beach, 1 v., leg. Schleich, VIII. 1981; São Nicolau, Tarrafal, 1 v., leg. Groh, XII. 1978; Ilha do Sal, Santa Maria, on beach, several juv. v.; Boavista, Sal Rei, 1 v.; Boavista, 1,4 miles W of Pta. Areia, 22 m, 4 v.; Boavista, off Praia Corralhino, 10 m, 1 v.; São Tiago, northern part of Baia de Sta. Clara, 15-35 m, 1 spm.; São Tiago, 14°54' N/23°30,5' W, 15 m, 1 v.; 15°16' N/23°47' W, 55-60 m, 1 v.; 15°13,2' N/23°46,3' W, 1 juv. v.; Fogo, SW of Sta. da Encarnação, 20-25 m, 1 juv. spm., 10 m, 1 juv. ch. all dredged R/V "Calypso", leg. MARCHE-MARCHAD, XI.1959; all MNHN. Senegal : Banc de Seminole, 43-45 m, 1 juv. spm., 3 v., leg. MARCHE-MARCHAD; Dakar, Bel-Air, Plage de la Marine, 2 sh., 3 v., leg. VON COSEL, 16.X.1988; Dakar-Hann, on beach, 1 sh., 3 v., R/V "Président Théodore Tissier", littoral station, 1936; Gorée, 1 spm., leg. GUILBERT, 7.II.1958; SE of Gorée, 14°41' N/17°23,3' W, 17-19 m, 1 spm., 5 v., dredged R/V "Louis Sauger", leg. VON COSEL, 24.III.1988; Cap Rouge, several juv. sh., Mission GRUVEL, III-IV. 1909; M'Bour, Petite Côte, on beach, 1 sh., 2 v., leg. von Cosel, 22.III. 1988; off M'Bour, 14°26,5' N/17°05,5' W, 10-11 m, 4 spm., 6 v.; off Saloum estuary, 14°2,5' N/17°09' W, 24 m, 2 v., both dredged R/V "Commandant Henri Gomis", leg. BODARD, 8.XII.1966; all MNHN. Guinea : Off Dubreka Estuary, 9°42' N/15°33' W, 35 m, 1 old valve which still shows colours; off Conakry, 9°30' N/15°09,6' W, 45 m, 1 old, apparently subfossil v.; off the border to Sierra Leone, 9°06' N/14°35' W, 52 m, 1 old, app. subfossil v.; all dredged R/V "André Nizery", leg. VON COSEL, 29-30.X.1988, all MNHN.

BIOTOPE : Arca noae lives mainly on hard grounds and is byssally attached on rocks, to the undersides of rocks and in crevices. On soft bottoms it can be found attached to isolated stones or other hard objects including the shells of larger gastropods. The bathymetric range is from low water to about 50 m.

REMARKS : See under Arca bouvieri.



FIG. 1-2. — 1 : Internal view of right valve of *Arca noae* L. Western Sahara. 2 : Internal view of right valve of *Arca bouvieri* Fischer. Angola. (Scales bars = 10 mm.)

Arca bouvieri P. Fischer, 1874 (Pl. I, 3A-D, 4; fig. 2; map 1)

Arca bouvieri P. Fischer, 1874 : 206. Arca sanctahelenae Smith, 1890 : 305, pl. 22, figs. 8-8b.

TYPE MATERIAL : The holotype (coll. BOUVIER) has not been isolated in the MNHN although ROCHEBRUNE (1881 : 250) cites it as "Sta. Vincent, Bouvier 1870, Mus. Paris." Two paratypes (complete specimens) from coll. PETIT DE LA SAUSSAYE are present and among them is the specimen figured by FISCHER (1876 : 239-240, pl. 8, fig. 2).

TYPE LOCALITY : Cape Verde Islands.

#### DESCRIPTION

Shell to 70 mm in length. Solid. Equivalve. Inequilateral, beaks in the anterior third. Outline subtrapezoidal, oblong, height relatively great. In large specimens : Posterior area relatively large; posterior angle rounded; posterior margin long, almost vertical, often straight some weakly auriculate. Median area as a shallow sinus, ventral margin more or less straight or with a shallow indentation at byssal gape. Anterior margin broadly rounded. Dorsal margin long, straight. In small specimens : Posterior area narrow; posterior angle carinate; posterior margin subacute, sloping inwardly, auriculate at junction with posterior carina. Median sinus marked; ventral margin indented. Anterior margin sloping inwardly, weakly indented. Dorsal margin relatively very long, lateral junctions acute. Dorsal area long, very wide and almost flat rising gently to low umbos. Ligament initially restricted to triangular area between beaks but eventually covering most of the dorsal area except for a narrow posterior strip and a very narrow anterior strip. Chevrons developing symmetrically at first but in gerontic examples becoming irregular and often very numerous.

Hinge plate very narrow. Teeth in two series, junction just behind the beaks and indistinct. Anterior set up to 40, posterior set up to 50 in number. All teeth finely serrated, postero-median teeth slightly chevron shaped, remainder more or less straight and vertical.

Sculpture primarily radial of ribs, riblets and raised threads. Juveniles which about 30-35 more or less uniform riblets except for those on the posterior area which are much larger. In large specimens : posterior and postero-median area with 8-10 rounded ribs with up to 6 raised threads in the interspaces. Median area with numerous riblets and raised threads. Anterior area with 4-6 ribs.

Periostracum mostly worn, retained around margins only in adult examples. Composed of very thin, subdiaphanous, straw coloured concentric lamellae, very weakly reinforced by radial thickenings and breaking down over ribs to give an apparent radial arrangement. In juveniles the carinal bristles are occasionally preserved, these are greatly expanded, irregularly spathulate and extremely fragile.

The external background colour of the shell is cream and is variously overlain with broad oblique, sometimes zigzag bands from brick red to purplish red in colour. Larger shells frequently have an orange tinge to the posterior area. Internal colour is mostly white except for a brickred marginal zone.

The adductor muscle scars are subequal, the posterior a little larger. The byssus retractor scar lies under the posterior part of the dorsal area, is an elongate triangle extending along two thirds of the posterior hinge plate.

SELECTED SHELL MEASUREMENTS : See in Remark section.

DISTRIBUTION : Senegal (Cape Verde Peninsula) to southern Angola (Moçamedes); Cape Verde Islands, São Tomé, Principe, Annobon; Ascension, St. Helena.

MATERIAL EXAMINED : Senegal : Dakar, SW of Madeleines Islands, 45-46 m, 3 juv. spm., 11 juv. v., leg. MARCHE-MARCHAD, 9.I.1954; Dakar, on Gouvernment Beach, 2 v., R/V "Président Théodore Tissier", littoral station, 1936; Dakar, SW of Cap Manuel, 50 m, 2 v., dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 20.II.1956; S of Gorée, 110-112 m, 1 juv. v., dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 18.II.1954; Gorée, 15-25 m, 11 spm., leg. PIN, 1987; Baie de Rufisque, 18-20 m, 1 juv. spm., 5 juv. v., Mission GRUVEL, II-IV.1909; off M'Bour, 14°2,5′ N/17°09′ W, 24 m, 6 spm., 1 v., dredged R/V "Commandant Henri Gomis", leg. BODARD, 7.XII.1966; M'Bour, on beach, 1 v., leg. VON COSEL, 22.III.1988; S-Casamance, off Cap Skirring, 12°25′ N/17°17′ W, 25 m, fine sand with stones, 1 spm., dredged R/V "Louis Sauger", leg. VON COSEL, 27.III.1988; all MNHN. Cape Verde Islands : (no precise locality), 1 sh., coll. DE CESSAC, 1874; São Vicente, 1 sh., 1 v., coll. MABILLE, 1905; S of Santa Luzia, 16°44′N/24°44,5′ W, 52 m, coarse sand with shells and stones, 1 juv. spm., 2 v., dredged R/V "Princess Alice II", 1901; Ilha do Sal, Pedra Lume, on beach, 1 juv. sh., coll. CADENAT; São Tiago, Praia, 14°53,7′ N/23°30,4′ W, 25-30 m, 4 juv. v., dredged R/V "Calypso", 17.XI.1959; Brava, SW of Punta Tantão, 20 m, 1 juv. v., dredged R/V "Calypso", 21.XI.1959; all MNHN. Guinea : off Rio Nuñez, 10°27′ N/14°16′ W, 41 m, coarse sand with stones, 4 spm., several v., both dredged R/V "André Nizery", leg. VON COSEL, 28-30.X.1988, both MNHN. Côte d'Ivoire : off Abidjan, 5°01,5′N/3°23,5′W, 70 m, sand



MAP 1. — Distribution of Arca noae (circles) and A. bouvieri (squares). The empty circle indicates a record of subfossil valves only.

with shells, 1 juv. v.; off Grand Bassam, 4°57' N/2°42' W, 40 m, 1 spm., 1 v., both dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 19-22.III.1964, both MNHN. Ghana : Cape Coast, 26-31 m, 1 juv. spm., leg. LE LOEUFF, 10.II.1968; 4°36,5' N/1°31' W, 50 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.V.1956, both MNHN. Nigeria : off Niger Delta, 4°00' N/6°11' E, 34 m, 3 spm.; 4°03' N/6°12' E, 32 m, 10 juv. v., both dredged R/V "Calypso", 26.V.1956, leg. MARCHE-MARCHAD, both MNHN. Ilha do Principe : Between Pta. da Mina and I. Santa Ana, 10-12 m, 1 spm., 1 sh.; 1°42,5' N/7°28' E, 21 m, algues calcaires, 1 spm.; 1°43' N/7°29' E, 37 m, 1 spm.; 1°43' N/7°28,4' E, 73 m, 1 spm., 1 v.; 1°33' N/7°31' E, 90 m, 1 juv. spm.; all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.VI-1.VII.1956, MNHN. São Tome : off Baia de Ana de Chaves, 5 m, calcareous algae, 1 spm.; off Praia Lagarto, 5-6 m, 1 spm.; off Diego Nuñes, 0°23' N/6°43' E, 30 m, 1 spm.; north coast.

0°25,5' N/6°40' E, 50 m, 1 juv. spm., all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 11-21.VI.1956; all MNHN. Annobon : (without precise locality), 60 m, 3 juv. sh., coll. CAVELIER DE CUVERVILLE, 1886; north of Santo Antonio, 23 m, calcareous algae, 2 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 4.VII.1956; all MNHN. Equatorial Guinea : Bata, 1 sh., coll. POBEGUIN, 1891, MNHN. Gabon : Pont-Gentil, Ile aux Pigeons, 3 m, on mangrove roots and *Pinna*, 5 spm., leg. CHEVALIER, 1984-89, MNHN. R. P. Congo : Pointe-Noire, plage Sauvage, 2 v., leg. VON COSEL, 10.XII.1985, MNHN. Angola : Barra do Dande, Bengo province, on rocks at low tide, 1 spm.; Cacuaco, Bengo province, on rocks at low tide, 1 spm.; 5-10 m, 9 juv. spm., 8 juv. v.; Ilha de Luanda, Luanda province, 40-60 m, 1 spm.; Corimba, Luanda province, 10-20 m, numerous spm.; Palmeirinhas, Luanda province, on rocks at low tide, 1 spm.; Cabo Ledo, Luanda province, 3 juv. spm., 3 juv. v.; Baia de Canoco, Benguela province, 2 juv. spm.; Praia Amelia, Moçâmedes, 40-60 m, 2 spm., all leg. GoFAS, 1981-86, MNHN.

BIOTOPE : Byssally attached on hard substrates such as rocks, stones, shell agglomerations and secondary hard substrates like shells or small stones on sand, mostly with calcareous algae. Bathymetric range from sublittoral to 60 m.

#### Remarks

Arca bouvieri and A. noae have overlapping ranges only in the Senegal and Cap Verde regions. They can be separated at all sizes by the differences in shell shape (fig. 3) and sculpture. Arca bouvieri is less elongate, more compressed and less inequilateral than A. noae. The radial ribs of A. bouvieri are much stronger especially over the posterior area.



FIG. 3. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of Arca bouvieri (n = 20) and Arca noae (n = 20).

Arca bouvieri belongs to the A. noae group of species which is represented in the Caribbean by A. zebra, in the Indo-Pacific by A. navicularis and in the Panamic Pacific by A. pacifica. A. bouvieri differs from all of these in its relatively short quadrate outline and the large difference between the median and lateral sculpture. In these respects it differs most from A. noae and is closer to A. zebra and A. navicularis.

We can find no reason to regard A. sanctahelenae Smith as distinct from A. bouvieri. It

would appear that SMITH (1890) overlooked FISCHER's species as he compares the St. Helena material only with A. noae and A. navicularis. LAMY (1907: 24) also considered A. sanctahelenae to be a synonym.

## Arca avellana turbatrix n. subsp.

(Pl. II, 1A-D, 2; fig. 7; map 2)

TYPE MATERIAL : Holotype (28.3 mm), MNHN, Santo Antonio, Benguela province, Angola; intertidal, rocks; leg. GoFAS. Paratypes MNHN : 2 spm. as holotype; 2 spm. Lucira, Moçâmedes province, Angola; NMWZ : 8 spm. Corimba, Moçâmedes province, Angola; all leg. GoFAS.

TYPE LOCALITY : Santo Antonio, Benguela province, Angola.

## DESCRIPTION

Shell to 35 mm in length. Equivalve. Inflated. Inequilateral, beaks in the anterior third. Outline subtrapezoidal, posterior area demarcated by a strong posterior angle which is often carinate. If small and not distorted then : longer than high; posterior margin obliquely truncate usually slightly auriculate, posterior ventral junction acute; ventral margin straight, gently curving or slightly indented by byssal gape; anterior margin broadly rounded; dorsal margin long straight, dorsal lateral junctions angular. Posterior area well demarcated by carinate posterior ridge, median sinus not apparent. If large then usually deformed to some degree and then : some remaining longer than high others almost as high as long; posterior margin obliquely subtruncate, posterior ventral junction angular or narrowly rounded; ventral margin variously indented byssal gape which may be extensive; anterior margin rounded, straight or irregular.

Dorsal area large, broadening rapidly with wide imbonal separation. Ligament extensive, covering dorsal area, chevrons irregular, developing rapidly and numbering up to 10 in gerondic specimens.

Hinge plate narrow, teeth small in two series but separation obscure, anterior set up to 38 teeth, posterior set up to 43 teeth. All teeth minutely serrated and with a frontal groove; posterior marginal teeth becoming chevron shaped, others straight and vertical.

Sculpture on posterior area of larger shells of 5-8 ribs, the first three from the posterior carina most prominent and usually at least one bifid. Towards dorsal margin ribs smaller, more variable in size, some as interspace riblets; of smaller shells usually of 4-5 simple ribs. Median area frequently divided by a weak posterior median ridge, posterior section with 15-20 nodulose riblets, anterior section and anterior area with 25-30 radial riblets variously with interspace radial threads. In most specimens the radial element is dominant but in more elongate examples the concentric element is equally expressed especially on the posterior median zone.

Periostracum rarely well preserved but usually present around byssal gape and remnants on posterior carina. Posterior carina with a single row of large, spathulate bristles which are smooth on the anterior edge and coarsely serrated on the posterior edge, they are thin, fragile and straw coloured (pl. II, 1A). On the posterior area short lamellar elements are present between the ribs and are reinforced by weak slightly emergent hairs. On the remainder it is concentrically lamellar but breaks down into radially arranged segments which are weakly reinforced emergent hairs.

Shell generally pale in colour usually with mauve-brown tinges along the posterior border, occasionally extending throughout the posterior third, over the hinge plate and onto the anterior area, some darker brown on posterior area. Mantle pigmentation absent except for the black eyespots.

SELECTED SHELL MEASUREMENTS : See figure 4.

DISTRIBUTION : From Guinea (Conakry area) south to Cameroon and Angola (Luanda).

MATERIAL EXAMINED : Senegal : S of Cap Skirring, S-Casamance, 2 worn v., on beach, leg. VON COSEL, 3-6.III.1988, MNHN. Guinea : Roume, Iles de Los, beach on the N-side, 2 v., leg. VON COSEL, 29.V.1988; Kassa, Iles de Los, E-Side, N of village, on the undersides of boulders and stones with very thin layer of mud on them, low tide, 2 spm., leg. VON COSEL, 12.XI.1988, both MNHN. Liberia : 5°21,5' N/9°54,5' W, 73-80 m, 1 v., dredged R/V " Calypso", leg. MARCHE-MARCHAD, 20.V.1956, MNHN. São Tome : Praia Emilia, under stones at low tide, 1 spm., leg. GOFAS, XI.1983, MNHN. Cameroon : Victoria (now Limbe), Morton Bay, 2 spm., 1 v; Mondoleh Island, Ambas Bay, 6 spm., all under stones at low tide, leg. VON COSEL, IV.1969 and XI.1985, MNHN. Gabon : Cap Esterias-Pointe Idolo, on stones in sand at low tide, 3 spm., 1 v., leg. VON COSEL, MNHN; (no precise locality), 6 spm., coll. H. FISCHER, MNHN. R.P. Congo : Pointe-Noire, Plage ORSTOM, 3-6m, many v.; Plage Mondaine, on beach, many v.; Songolo, 3-5 m, 3 v.; Plage Sauvage, on beach, 3 v., all leg. VON COSEL, XI-XII.1985; Pointe-Noire, 6 spm., 6 v., coll. Office Pte.-Noire; Pointe-Noire, 5 spm., coll. AUBERT DE LA RUE; all MNHN. Angola : Ambrizete, Zaïre province, 1 spm., 1 v.; Barra do Dande, Bengo province, 6 spm.; Cucuaco, Bengo province, 1 spm.; Praia Etambar, Corimba, Luanda province, 10 spm.; Caotinha, Benguela province, 4 spm., all leg. GOFAS, MNHN.

**BIOTOPE**: Byssally attached to stones and rocks, mostly on the undersides. This species appears to prefer more or less turbid waters and is also found in areas with slightly reduced salinities during the rainy season. Bathymetric range from low intertidal to sublittoral.

DERIVATIO NOMINIS: *turbatrix*, Latin, f. the "disturber" or "trouble maker" making reference to the systematic confusion prevalent in this group of species.

#### Remarks

This is the tropical West African species referred to as *Arca imbricata* Bruguière of authors. Its identity has never been examined in any detail and it is assumed that it was identified as that species on geographical considerations alone. The distinctions between the Caribbean form known as *A. imbricata* and its Indo-Pacific counterpart. *A. avellana* Lamarck are similarly obscure. We have examined these in relation to the West African form and make the following observations :

CHARACTER	Indo-Pacific	WEST AFRICAN	CARIBBEAN	
Size	To 50 mm.	To 35 mm.	To 65 mm.	
Posterior sculpture	Ribs often irregular, occasionally bifid.	Ribs often irregular, usually bifid.	Ribs mostly regular, rarely bifid	
Periostracal insertion marks	Lacking	Lacking	Present	
Ligament chevron N°	Medium	High	Low	
Umbonal separation	Wide	Very wide	Moderate	
Carinal bristles	Large, fragile straw coloured	Large, fragile straw coloured	Very large, robust greyish	
Internal shell colour	Usually partly white	Mostly white	Usually dark overall	
Mantle colour	Patterned shades of brown	White except for eye spots	Patterned shades of brown	

Arca avellana (Indo-Pacific) (pl. II, 4) : This form has a larger maximum size but the general form of the shell, sculpture and periostracum are so similar that we are unable to identify significant differences. Only the umbonal separation and relative number of ligament chevrons show a difference (figs. 5 & 6). The colouration pattern is similar but there does seem to be a greater incidence of dark coloured specimens from the Indo-Pacific and this may also be reflected in the greater pigmentation of the mantle.

Arca imbricata (Caribbean) (pl. II, 3A-B) : The Caribbean form attains a much larger maximum size and in general is much less distorted. The shells are frequently more elongate and the ribs on the posterior area are rarely bifd but bear short grooves which represent the insertion points of the periostracal bristles. Umbonal separation is relatively small and the number of ligament chevrons is relatively fewer. The internal colouration is frequently darker with most specimens coloured throughout and many being chocolate brown or black. Most significantly however are the carinal periostracal bristles which are approximately twice the size, more strongly reinforced and more persistent (pl. IX, B).

From these comparisons it would appear that the West African form is more closely allied to that of the Indo-Pacific than it is to that of the Caribbean. However we have not addressed the possibility that these differences are merely ecophenotypic or of regional significance only. We suggest that as the total range of variation is not seen in all three groups that there is at least some regional significance. Even so this may reflect the absence of certain habitats in a region and in West Africa the exclusion of coral reef communities may be important. The habitats described here of the West African population are unusual in that the preference seems to be for turbid intertidal areas which are in contrast to the coral reef association with clear water in the tropical regions of the Caribbean and Indo-Pacific. Of the characters cited we view the carinal bristles to be most relevant as it is difficult to envisage the functional significance of the differences noted. The umbonal separation and ligament chevrons are related to growth with both having an allometric relationships to shell size (THOMAS, 1976;



FIG. 4-6. -4: Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Arca avellana turbatrix* (n = 25). 5: Graphs of Umbonal separation plotted against Shell Length for four samples of the *Arca imbricata* complex. Florida and Guadeloupe are *A. imbricata*, Seychelles is *A. avellana* and West Africa is *A. a. turbatrix*. 6: Graphs of ligament chevron number plotted against shell length for four samples of the *Arca imbricata* complex. Florida and Guadeloupe are *A. imbricata*, Seychelles is *A. avellana* and West Africa is *A. a. turbatrix*.

OLIVER and ALLEN, 1980). The differences observed in these could be related to growth rate and if the West African population was restricted to less favourable conditions the allometry would then occur in the smaller size classes. The only meaningful way forward would be to carry out studies related to the genetic make up of each population but this is beyond the scope of the material at hand.

Resorting to traditional techniques we conclude that the West African form is most closely allied to that of the Indo-Pacific but the differences observed may be due to regional environmental conditions. However both populations are geographically isolated as the Indian Ocean populations do not spread beyond the province of Natal and the West African form is restricted to the Gulf of Guinea north of Namibia. Consequently we have given subspecific status to the West African form as *A. avellana turbatrix* but not in keeping with tradition regard it as distinct from the Caribbean form *A. imbricata*. If one views the differences to be insignificant then one cannot regard the Caribbean and Indo-Pacific forms to be distinct either

and neither would the distinction of the Panamic Pacific form known as *A. mutabilis* be justifiable. The whole complex would then have to be regarded as a single cosmopolitan species taking the earliest name of *A. imbricata* Bruguière. This is the position adopted by LAMY (1907 : 26-38) but he accepted three varieties within the Indo-Pacific ad West African ranges, namely var. *arabica* Philippi, var. *avellana* Lamarck, and var. *martensi* Dunker. He also isolated the Caribbean form as the nominate species *A. imbricata*.



FIG. 7-8. — 7 : Internal view of right valve of Arca aveilana turbatrix n. ssp. Angola. 8 : Internal view of right valve of Arca retragona Poli. Ireland. (Scales bars = 5 mm.)

Arca tetragona Poli, 1795 (Pl. II, 5A-B, 6; fig. 8; map 2)

Arca tetragona Poli, 1795 : 137.

TYPE MATERIAL : Not located.

TYPE LOCALITY : Sicily.

#### DESCRIPTION

Shell to 40 mm in length. Equivalve. Inflated if growth is unhindered but may be compressed if constricted in crevices. Inequilateral, beak position variable, in the anterior third in regular specimens but only just in front of the mid line in some distorted examples.

Outline subtrapezoisal, angular, juveniles elongate, adults irregular oblong. Posterior area narrow, well demarcated by the posterior angle which remains sharply carinate; posterior margin oblique, more or less straight, some very weakly auriculate. Median area not depressed, ventral margin gently curved or sinuate at byssal gape. Anterior margin rounded, variable. Dorsal margin long, straight.

Dorsal area wide to very wide, usually flat but may be cleft in distorted examples; umbos very low. Ligament with unusual growth pattern; initially with two strips of fibrous ligament radiating from the beaks, between these and to either side of them the dorsal area is free of ligament material. Lamellar chevrons are added mostly within the anterior strip then to the posterior strip and finally new sites of ligament growth appear along the hinge line between the

original strips so that in the largest shells most of the dorsal area is covered. The chevrons are very narrow and may reach 25 in number.

Hinge plate narrow, teeth in two series, separation obscure at a point behind the umbonal line; anterior set up to 30 teeth, posterior set up to 15 teeth. Teeth minutely serrated anterior teeth small, some chevron shaped, mostly vertical but marginal teeth oblique; posterior teeth straight but becoming progressively oblique towards the margin where they are subparallel.

Sculpture of radial riblets and raised threads, initially with 4-5 riblets on the posterior area and 30-35 finer riblets on the remainder, carinal riblet bifid often imbricate. Subsequently posterior riblets divide and are added to by interspace threads. Median area with closely spaced, somewhat acute riblets contrasting slightly with the more rounded and slightly broader riblets on the anterior area.

Periostracum usually lost, persistent around margins and on the posterior area only. Composed of concentric lamellae reinforced by bristles arising from the riblet interspaces, most often the lamellar part is worm and the arrangement appears simply radial. The bristles become spicate on the postero-median and posterior areas. The carinal bristles are large, lanceolate but with irregular margins. All the bristles are dark coloured from brown to black.

Shell colouration is weak, mostly greyish white but with some brown tinges internally over the posterior area.

Adductor scars small, subequal; both with myophoric ridges extending into the umbonal cavity. Byssal retractor small, triangular restricted to the posterior half of the shortened posterior hinge plate.

DISTRIBUTION : Shetlands to Morocco (Essaouira/Mogador), the Azores and throughout the Mediterranean.

MATERIAL EXAMINED : Ireland : St. Johns Pt., Donegal, 5 spm., leg. P. G. OLIVER, Berehaven, Bantry Bay, 9 spm., leg. J. T. MARSHALL; both NMWZ. England : Falmouth, leg. J. T. MARSHALL, 8 spm., NMWZ. Celtic Sea : 8 stations between 49°15′ and 48°33′ N and 05°09′ and 05°28,5′ W, 102-112 m, 15 v., all dredged R/V "Thalassa", leg. von Cosel, XII.1983, MNHN. Atlantic France : Brest, Finistère, 2 sh.; Lorient, Morbihan, 3 spm.; Belle-Ile, Morbihan, 1 sh.; Le Croisic, Loire-Atlantique, 4 spm.; Ile d'Yeu, Vendée, 2 spm.; Ile d'Oléron, Charente-Maritime, 3 spm., all. coll. LOCARD, 1982; Golfe de Gascogne (Biscay), 18 spm., coll. DENIS; Arcachon, Gironde, 1 spm., coll. ROCHE, 1894; St-Jean-de-Luz, Basses-Pyrénées, numerous sh. and v., coll. H. FISCHER, 1898; all MNHN. Atlantic Spain : Ceuta, Strait of Gibraltar, Punta Almina, 25-40 m, 6 spm., 1 v., leg. BOUCHET, GOFAS & LOZOUET, V.1986, MNHN. Algeria: Oran, 40 m, 2 spm., 2 sh., coll. PALLARY; 60 m, 3 spm., coll. LOCARD, 1892; Alger, 4 juv. sh., 1 v., old coll., all MNHN. Italy : Palermo, Sicily, 11 spm., 3 sh., coll. JOUSSEAUME, 1916; 3 spm., 2 sh., coll. Allery, 1872; 7 spm., coll. Monterosato, 1906; Naples, 5 spm., 4 sh., coll. Petit, 1873; 4 spm., 2 sh., old coll.; 1 v., coll. MONTEROSATO, 1906; Capri, 3 spm., coll. LOCARD, 1892; all MNHN. Mediterranean France : Nice, Alpes-Maritimes, 1 spm.; St. Raphaël, Var, 3 spm.; St. Tropez, Var, 2 spm., all coll. LOCARD, 1892; Toulon, Var, 1 spm., old coll.; Marseille, Bouches-du-Rhône, 9 spm., coll. Locard, 1892; 1 spm., coll. Vayssière, 1907; Sète, Hérault, 2 spm., coll. Locard, 1892; Banyulssur-Mer, Pyrénées-Orientales, 8 spm., coll. Lab. Arago, 1904; 4 spm., old coll., all MNHN. Corsica : St. Florent, N-coast, 2 spm., coll. LOCARD, 1892, MNHN. Atlantic Morocco : Mogador (now Essaouira), 6 spm., coll. PALLARY, MNHN. Azores : Ponta Delgada, São Miguel, 10-20 m, 2 spm., 5 v., leg. BOUCHET, 9-15.VII.1983, MNHN. 25 lots with numerous spm., sh. and v., from São Miguel, Terceira, Faial channel and Flores, between 39 and 225 m, empty shells and valves washed down on the steep slope to 1675 m, all dredged R/V "Jean Charcot", BIACORES-Expedition, leg. MÉTIVIER, X.1971, all MNHN.

BIOTOPE : Byssally attached to rocks in crevices or in more open situations in tranquil sites such as those at depth. Bathymetric range from low in the intertidal to 100 m.



MAP 2. - Distribution of Arca avellana turbatrix (circles), A. a. avellana (shaded area) and A. tetragona (squares).

**REMARKS**: This species probably cannot be considered to be a component of the tropical West African fauna but as it can be confused with *Arca avellana turbatrix* and juveniles of *Arca noae* we have included it here. Even when distorted it can be easily separated on the form of the ligament and periostracal bristles.

## Genus ACAR Gray, 1857

TYPE SPECIES : Arca gradata Broderip and Sowerby, 1829 (SD Woodring, 1925).

Acar cf. plicata (Dillwyn, 1817) (Pl. II, 7A-B; fig. 10; map 3)

Arca plicata Dillwyn, 1817 : 227-228.

TYPE MATERIAL : Based on the figure in CHEMNITZ (1795 : 244, pl. 204, fig. 2008).

TYPE LOCALITY : Red Sea.

## DESCRIPTION

Shell to 26 mm in length. Equivalve. Initially slightly compressed but soon becoming rather tumid to very tumid in gerontic specimens (the onset of the gerontic expansion can occur in a wide range of sizes). Inequilateral, beaks in the anterior 1/4 rather low.

Outline subrectangular-subtrapezoidal, anteriorly usually slightly narrowed; frequently distorted especially in gerontic examples. Posterior area narrow, demarcated by a persistent posterior carinal ridge; posterior margin oblique, posterior ventral junction subacute. Median area flat to weakly sulcate; ventral margin more or less straight but often sinuous; byssal gape obsolete or very narrow. Anterior area small, demarcated by a rounded ridge; anterior margin broadly rounded. Dorsal margin straight.

Dorsal area usually very narrow, wider anterior to the beaks but becoming wide overall in gerontic specimens; umbonal separation usually slight. Ligament restricted to well behind the beaks, chevrons very narrow, numbering up to 8 in normal specimens but as many as 20 in gerontic examples.

Hinge plate narrow to moderate, teeth in 2 series but separation obsolete except in old specimens where ligament growth has eroded the small central teeth; anterior set up to 10 teeth, posterior set up to 15 teeth. Teeth strong, anterior laminar, posterior chevron shaped, all coarsely serrated, marginal teeth becoming very oblique. In gerontic specimens the teeth may be irregular, often divided medially.

Sculpture imbricate, of up to 30 rather broad concentric ridges dissected by 25-35 radial ribs these dividing during growth to number up to 50. The resulting vesicular nodes are smoothly rounded except on the posterior angle where they may be incomplete and therefore slightly plicate. The posterior area bears 5-7 strong ribs on which the nodes are greatly swollen

giving the cross section of the posterior margin a strongly corrugated appearance. This is a little less so for the Cape Verde Islands material.

Periostracum very thin, rarely retained.

Shell whitish, exterior rather dirty cream; interior of Cape Verde, São Tomé and Annobon specimens mostly flushed with pale orange/pink, the Angolan material rarely so.

Adductor scars more or less equal, raised with myophoric flanges along their inner edges. Inner lateral margins crenulate, ventral margin weakly so or irregularly denticulate.

SELECTED SHELL MEASUREMENTS : See figure 9.



FIG. 9. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Acar* cf. *plicata* from West Africa (n = 24).

DISTRIBUTION : This species occurs from the Cape Verde Islands south to Angola but it is most common on the Cape Verde Islands, the islands in the Gulf of Guinea and on the coast of Angola.

MATERIAL EXAMINED : Cape Verde Islands : (no precise locality), numerous spm. and v., leg. RANG, 1837; 4 spm., coll. DE CESSAC; 5 spm., coll. BOUVIER; Santo Antão (no precise locality), 5 v.; São Vicente, Baia Matiota, Mindelo, on the undersides of stones, 1-2,5m, 3 spm., 2 v.; São Vicente, Baia Porto Grande, 2 sh., 10 v., both leg. VON COSEL, XII.1978; Ilha do Sal, (no precise locality), numerous spm., sh. and v., leg. CADENAT, 1950; Ilha do Sal, Palmeira, undersides of rocks at low tide, 7 spm.; Ilha do Sal, Baia Algodoeiro, on beach, 4 v.; Ilha do Sal, Santa Maria, underside of boulders 2-3 m, 3 spm., all leg. von CoseL, 15.XII.1978-1.1.1979; Ilha do Sal, 16°35'N/22°55' W, calcareous algae, 15 m, 1 spm., dredged R/V "Calypso", 26.XI.1959; Boavista, Gatas (Punta Rodrigo), on the undersides of stones on mixed sand, 1,5-2m, 6 spm., leg. von Cosel, 27.XII.1978; São Tiago, Praia, 8 v., leg. CADENAT, 1950; São Tiago, Porto de Praia, four lots with 3 spm. and 7 v., from 2 to 30 m, all dredged R/V "Calypso", 17-19.XI.1959; Brava SW of Punta Tantão, 20 m, 3 v.; Fogo, SW of Santa da Encarnação, 20-25 m, 12 spm.; Fogo, Punta da Araia, 2.5 m, 2 spm. both dredged R/V "Calypso", 20.XI.1959; all MNHN. Senegal : Dakar, SW of Cap Manuel, 50 m, 1 v.; Dakar, 129-150 m, 1 v., both dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 1956 and 1958, MNHN, Liberia : 5°21,5' N/9°54,5' W, 73-80 m, 4 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 20.V.1956, MNHN. Côte d'Ivoire : Abidjan region (no precise locality), 2 v., leg. LE LOEUFF, MNHN. Ilha do Principe : W-coast, 1°37' N/7°22' E, 30 m, 1 v.; Baia de Santo Antonio, between Punta da Mina and Punta de Novo Destino, 6m, 1 v.; Baia Santo Antonio, between Punta da Mina and Ilheu Santa Ana, 10-12 m, 1 spm.; both dredged R/V "Calypso", leg. MARCHE-MARCHAD, VI.1956, MNHN. São Tome : Punta Diogo Vaz, west coast, 30m, 1 spm.; 1°38,4' N/7°22,1' E, 31 m, 1 spm.; off S. Tomé city, 0°20' N/6°45' E, 10 m, 2 spm., 5 v.; off Praia Lagarto,



MAP 3. — Distribution of Acar cf. plicata (circles), A. plicata (shaded area) and A. pulchella (squares).

5-6m, 5 spm., all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 11-27,VI,1956; all MNHN. Annobon : N of Santo Antonio, 23 m, 1 spm.; 1°25,2′S/5°36,1′E, 20 m, 1 spm., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, VI and VII.1956; 1°24′S/5°37,5′E, 20-40 m, 1 spm., 1 v., leg. CROSNIER, 11.XII.1965; 1°28,5′S/5°37,5′E, 35-55 m, 3 spm., leg. POINSARD, 16.VI.1967; all MNHN. **R.P.** Congo : Pointe-Noire, Plage Mondaine, N of lighthouse, low tide, 7 v.; Plage Sauvage, on beach, 1 v.; Plage ORSTOM, coarse sand and stones, 5-7 m, 1 v., all leg. von CosEL, XI-XII.1985, all MNHN; Loango, 4 v., leg. Office Pointe-Noire, 1969, MNHN. Angola : Cabo Ledo, Luanda province, 10-40 m, 2 spm.; Praia Etambar, Corimba, Luanda province, rocks, infralittoral, many spm.; Baia do Mussulo, Luanda province, 5 spm.; Baia de Santa Maria, Benguela province, rocks, 0-2 m, 18 spm.; Caotinha, Benguela province, rocks, infralittoral, 7 spm.; Baia do Limagem, Benguela province, rocks, 0-2 m, 1 spm.; Baia de Lucira (Bissonga), Moçâmedes province, intertidal, 4 spm.; Lucira (Praia do Cesar), Moçâmedes province, infralittoral, 3 spm.; Praia Amelia, Moçâmedes province, rocks, infralittoral, 2 spm., all leg. S. GoFAS, 1982-1984, MNHN.

BIOTOPE : This species lives in crevices and under rocks where it is attached by a weak byssus. It is found from low in the intertidal to 40 m.



FIG. 10. — Internal view of right valve of Acar cf. plicata (Dillwyn). São Tomé. (Scale bar = 5 mm.)

## Remarks

The genus *Acar* is distinctive with its coarse imbricate sculpture and raised muscle scars but the species systematics are very complex. Traditionally the species are identified on their geographic distribution such that *A. plicata* is Indo-Pacific, *A. pulchella* (Reeve, 1844) is Mediterranean, *A. domingensis* (Lamarck, 1819) is Caribbean and *A. gradata* (Broderip & Sowerby, 1829) is Panamic. The West African form has been known by all but the Panamic name. Rost (1955) in discussing *A. gradata* mentioned the coarse and fine sculptured varieties of that species and we have observed the same feature in the Caribbean *A. domingensis* but not to any great extent in the West African form. Even in the coarse sculptured form of *A. domingensis* the nodes never appear to be so inflated as in the West African material and the posterior ribs are finer or lower. The orange/pink colouration is apparently absent from Caribbean material. In sculptural coarseness the Indo-Pacific *A. plicata* is very similar but generally as the name implies the concentric elements are more lamellar especially on the posterior angle which often appears foliate. The posterior ribs are similar in development but The distinctions rest therefore on the coarseness of the sculpture and the degree to which the radial and concentric elements fuse into either vesicular nodes of fluted lamellae. Given the great range in variation we are refraining from giving the West African material separate nomenclatural status. From our observations the similarities in coarseness of sculpture, distinctiveness of the posterior ribs, size and colour we conclude that the West African form is closer to that of the Indo-Pacific. MEYER (1868) in discussing the Tertiary forms of *Acar* suggested that *A. clathrata* (Defrance, 1816) was replaced by the Recent *A. pulchella*. In general form the Pliocene species is close to *A. plicata* and could also be the fossil equivalent of the West African form. We recognise the affinity of the West African and Indo-Pacific forms by using the name *A. plicata*.

## Genus BARBATIA Gray, 1842

TYPE SPECIES : Arca barbata Linné, 1758 (SD Gray, 1857).

**Barbatia complanata** (Bruguière, 1789) (Pl. III, 1A-B, 2, 3, 4, 5A-B; fig. 6; map 4)

Arca complanata Chemnitz, 1784 : 198, pl. 55, fig. 544. Arca complanata Bruguière, 1789 : 100. Arca stigmosa Dunker, 1853 : 46, pl. 9, figs. 8-11.

TYPE MATERIAL: The type is based on the figure given by CHEMNITZ (1784) and the specimen may be in the ZMC, Copenhagen. The type of *A. stigmosa* is probably in ZMB Berlin.

TYPE LOCALITY : This is cited as "Guinea" by CHEMNITZ which refers to tropical west Africa. BRUGUIÈRE cites Madagascar and O. Americano but this is erroneous and arises from the early belief that there was only a single pan-tropical species.

## DESCRIPTION

Shell to 50 mm in length but usually not exceeding 35 mm. Equivalve. Compressed. Inequilateral, beaks in the anterior third.

Outline subrectangular-subtrapezoidal, often somewhat distorted (some to the extent of being subtrigonal), the anterior usually a little narrower. Posterior area poorly demarcated by a low weakly angled posterior ridged but more noticeably by the change in the size of the ribs; posterior margin oblique, more or less straight to gently curved, posterior ventral junction roundly subacute. Median area weakly sulcate; ventral margin subparallel to dorsal margin to inclined towards the anterior, more or less straight or indented or distorted especially at byssal

gape which is rather long but not very wide. Anterior area small, demarcated by a weak rounded ridge, anterior margin broadly rounded but often restricted and the oblique, slanting inwards. Dorsal margin long, straight.

Dorsal area narrow to very narrow, becoming deeply cleft, umbonal separation slight. Ligament initially opisthodetic, rapidly the dorsal area and extending anteriorly well beyond the beaks; chevrons narrow, numerous in gerontic specimens, numbering up to 12.

Hinge plate rather narrow especially centrally, teeth in two series which are almost inseparable, total teeth count up to 45. Central teeth very small, often destroyed by ligament incursion, lateral teeth laminar or chevron shaped, becoming strongly oblique.

Sculpture of numerous radial riblets and ribs; posterior area with 6-7 large ribs often with 1-3 small secondary riblets. In some, the primaries are bifid, not greatly elevated, well spaced and evenly dissected giving the appearance of a twisted rope; anterior and median areas with 55-60 primary riblets, the anterior and those adjacent to the posterior angle a little larger than the more closely spaced median riblets, posterior median riblets bifurcating at an early stage. All radial elements dissected by concentric element and therefore appearing nodulose, concentric element also present as widely spaced low ridges caused by the enlargement of the nodules at regular intervals, these correspond with the concentric rows of larger periostracal bristles.

Periostracum with a primarily concentric arrangement of raised lamellae strengthened by slightly emergent bristles arising from the interspaces; the lamellae usually break down into rectangular sections to give a frilled appearance; lamellae pale straw coloured, emergent bristles brown giving a very characteristic pattern.

Shell white.

Adductor scars subequal the posterior a little larger, posterior pedal/byssal retractor scar small, elongate. Inner margin finely crenulate.

#### SELECTED SHELL MEASUREMENTS : See figure 11.

DISTRIBUTION : This species ranges from Guinea (Conakry area) and the Cape Verde Islands (where it is rare) south to southern Angola and is also found in São Tome, Principe and Annobon.

MATERIAL EXAMINED : Cape Verde Islands : Ilha do Sal (no precise locality), 1 dwarf spm., leg. CADENAT, IV-VI.1950, MNHN. Guinea : Kassa, Iles de Los, E-side, N of village, on the underside of a stone, at low tide, 1 spm., leg. VON COSEL, 12.XI.1988, MNHN. Liberia : 6°40' N/11°23' W, 51 m, 1 juv. v. dredged R/V "Calypso", leg. MARCHE-MARCHAD, 19.V.1956, MNHN. Côte d'Ivoire : off Tabou, 4°16,5' N/7'30' W, hard bottom, 40 m, dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 8.IV.1964; Abidjan region, "Palm Beach", on rocks, 6-10 m, 1 spm.; Canal de Vridi, Abidjan, 6 spm., 1 sh., 3 v.; Abidjan, SE of "2 Poteaux", on sandstone, 37 m, 1 juv. spm., all leg. LE LOEUFF, 1967-1973; all MNHN. Ghana : Cape Coast, hard bottom, 26-31 m, 1 spm., leg. LE LOEUFF, 10.II.1968; 4°37' N/0°50' W, 90-100 m, 3 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.V.1956, both MNHN. Togo : 6°10' N/1°37' E, 19 m, 2 juv. spm., leg. CROSNIER, 26.VII.1964, MNHN. Benin : Ouidah, 6°10' N/2°05' E, 100m, 5 juv. v., leg. MARCHE-MARCHAD, 22.XI.1958, MNHN. Nigeria : off the Niger delta, 4°00' N/6°11' E, 34 m, on *Chama*, 1 juv. spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 26.V.1956, MNHN. Cameroon : Victoria (now Limbe), Morton Bay, E-side, between rocks at low tide 14 spm., leg. von COSEL, I-3.XII.1985; Mondoleh Island, Ambas Bay, under and between stones near low tide, numerous spm., leg. von COSEL, IV.1969; Kribi, on beach, 8 v., leg. NICKLÈs, 1947; 3 spm., leg. VON COSEL, IV.1969; off Kribi, 2°36,8' N/9°46' E, 1 spm.; 2°33,3' N/9°42,6' E, 1 spm., 1 sh., 8 v.; Baia das Agulhas, 4-8 m, 1 spm.; 1°37' N/7°22' E, 30 m, 3 juv. v.; 1°42' N/7°28,8' E, 37 m, 1 spm.;



FIG. 11. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia complanata* from West Africa (n = 14).



MAP 4. - Distribution of Barbatia complanata.

1°20,7' N/7°17,6' E, 25-40 m, 1 dwarf spm., all dredged R/V "Calypso", leg. MARCHE-MARCHAD, 25.VI-1.VII.1956; all MNHN. São Tome : Esprainha, near Neves, 3 spm.; Praia Morro Peixe, 1 spm.; Praia das Conchas, 2 spm.; Praia Emilia, several spm., all between and under rocks at low tide, leg. GOFAS, XI.1983; Punta Diego Vaz, 0,6 m, 3 spm.; Ilheu das Cabras, 1 sh., off Pta. Diogo Nuñes, 4 m, 1 spm.; off Praia Lagarto, 5-6 m, 4 spm., 5 juv. v., all R/V "Calypso", leg. MARCHE-MARCHAD, 6-11.VI.1956; all MNHN. Annobon : 1°24' S/5°37,5' E, 20-40 m, 2 spm., leg. CROSNIER, 11.XII.1965; 1°24' S/5°36,7' E, 10 m, 1 spm.; 1°25,2' S/5°36,1' E, 20 m, rocks with calcareous algae, 2 spm., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, 13.VI.1956; all MNHN. **Gabon**: off Port-Gentil, on oil platform anchor, 30 m, 1 spm., leg. CHEVALIER, 1987; Port-Gentil, 2 spm., coll. Office Pte-Noire, both MNHN. **R.P. Congo**: Pointe-Noire, Plage Mondaine, on beach. 1 v., leg. von CoseL, XII.1985, MNHN. **Angola**: Cabo Ledo, Luanda province, 10-40 m, 1 sh.; Caotinha, Benguela province, 10 spm., 1 sh.; Baia Azul, Benguela province, rocks at low tide, 4 spm., 1 sh.; Baia do Limagem, Benguela province, rocks, 0-2 m, 1 spm.; Baia de Santa Maria, Benguela province, rocks 0-2 m, 3 spm., 1 v.; Baia da Lucira (Bissonga), Moçâmedes province, rocks at low tide, 1 spm.; Lucira (Praia do Cesar), Moçâmedes province, 3 spm.; Chapeu Armado, Moçâmedes province, rocks at low tide, 5 spm.; Praia Amelia, Moçâmedes province, rocks at low tide, 3 spm., all leg. GoFAS, 1982-85; all MNHN.

BIOTOPE : Byssally attached to rocks, stones, shells and other hard objects, from low tide about 40 m.

#### Remarks

This species despite its variability should not be confused with other west African species of *Barbatia* as it is the only species with the distinctive well spaced concentric ridges which give the periostracum a frilled appearance. It is also the only species to be encountered in the rocky lower intertidal and sublittoral.

We investigated the possibility that as in the Indo-Pacific there might be two closely related species equivalent to *B. foliata* (Forsskål, 1775) and *B. decussata* (Sowerby, 1833). Despite the variability in form of the west African specimens we could find no indication of pattern except that crevice dwelling examples were usually fore shortened or distorted.

Barbatia complanata belongs to the group of species represented by B. candida (Helbling, 1779) in the Caribbean, by B. foliata (Forsskål, 1775) in the Indo-Pacific and by B. reeveana (d'Orbigny, 1846) in the Panamic province. The west African species differs in having a much finer sculpture with approximately twice as many anterior and median primary riblets and in the posterior riblets narrower, more regular and numbering from 6-7 rather than the 3-4 typical of the Caribbean species. The periostracum of B. candida is heavier and the emergent bristles are consequently much longer and more robust. The Indo-Pacific B. foliata is an altogether much larger species with a more coarse sculpture which lacks the regular, well spaced concentric ridges. The west African species is therefore closer to that of the Caribbean.

American authors place these species in the subgenus *Cucullearca* Conrad, 1865. These species are distinct from those of *Barbatia* sensu stricto such as *B. barbata* and *B. gabonensis* (see below) but we are not certain of the affinities with other, mainly Indo-Pacific, groups and refrain from using this taxon until a more thorough revision is completed.

## Barbatia gabonensis n. sp.

## (Pl. III, 6A-B; fig. 14; map 5)

TYPE MATERIAL : Holotype (27.7 mm), MNHN, off Mayumba, Gabon, 3°25' S/9°56' E, 100 m, trawled R/V "Thierry", Guinean Trawling Survey, Sta. 58/6, 30.X1.1963. Paratypes : NMWZ, Ilha de Luanda, Angola, 90 m, 1 spm., leg. GOFAS; MNHN, off Grand Bassam, Côte d'Ivoire, 5°00' N/3°23' W 100 m, 1 spm., trawled R/V "La Rafale", Guinean Trawling Survey, Sta. 26/6.

TYPE LOCALITY : Mayumba, Gabon.



FIG. 12. — Internal views of right valves of *Barbatia complanata* (Bruguière) : A, Côte d'Ivoire; B, Angola. (Scale bar = 10 mm.)

## DESCRIPTION

Shell to 30 mm in length, not very thick for the genus. Equivalve, not inflated. Inequilateral, beaks in the anterior quarter.

Outline roughly rectangular, longer than high, length : height ratio from 2.2-2.6 : 1, dorsal and ventral margins more or less parallel. Posterior area indistinct; posterior angle smoothly rounded; posterior margin oblique, gently curving to posterior ventral junction which is narrowly rounded or subacute. Median area flattened or weakly depressed; byssal gape very narrow, short; ventral margin gently curved to straight, byssal sinus if present, weak. Anterior margin in smaller shells broadly rounded; later becoming more straight, oblique with a narrowly rounded anterior ventral junction. Dorsal margin moderately long, more or less straight.

Dorsal area very narrow, cleft; umbonal separation slight. Ligament restricted to area between and behind the beaks, chevrons narrow, numbering up to 7.

Hinge plate moderately thick, teeth in two series which are barely separable but the junction lies below the beaks, anterior set up to 10 teeth, posterior set up to 16 teeth. Teeth serrated, straight or slightly chevron shaped, becoming a little oblique towards the margins of the plate.

Sculpture fine of nodulose radial riblets, 90-110 in number more or less uniform in size with the exception 13-18 pairs of larger riblets which border distinct radial grooves.

Periostracum mostly lamellar except for long, subtubular, semispathulate bristles arising from the radial grooves. Lamellae straw coloured, bristles dark brown.

Shell mostly white, some with faint tinges of brown or brownish pink colour.

Adductor scars subequal, the posterior a little longer, posterior pedal/byssal retractor long and very narrow.

— 316 —

Length (mm)	Height (mm)	Tumidity (mm)	Anterior margin to beak (mm)	Rib No.	Groove No.
26.9	16.1	12.1	8.3	92	13
29.9	16.9	13.5	7.6	105	17
22.0	11.8	8.7	5,6	100	16
23.5	13.2	10.2	6.4	98	16
26.2	15.6	10.7	7.7	108	15
21.5	15.6	8.4	5.9	109	18

SELECTED SHELL MEASUREMENTS

DISTRIBUTION : Barbatia gabonensis is an entirely tropical species with a restricted distribution from Liberia south to northern Angola.



FIG. 13. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia gabonensis* from West Africa.

MATERIAL EXAMINED : The type material; Liberia : 4°37' N/10°50' W, 90-100 m, 2 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 24.V.1956, MNHN. R.P. Congo : off Pointe-Noire (no precise locality), 1 spm., leg. MARCHE-MARCHAD, MNHN.

BIOTOPE : Barbatia gabonensis is a deep water form with the present data indicating a range around 100 m. The byssus is functional although small and this suggests that this species lives attached to rock, stones or other hard substrates. The byssus is much weaker than in related forms from the littoral and sublittoral zones further suggesting that the local conditions are tranquil or sheltered. This could be explained by the lack of wave action at the depths from which *B. gabonensis* has been recovered.

DERIVATIO NOMINIS : gabonensis from Gabon, the country where the type locality is situated.

REMARKS : The immediate distinctive feature of this species is the series of radial grooves and the long periostracal bristles arising from them. This distinguishes it from the *Barbatia* 



MAP 5. — Distribution of Barbatia gabonensis (circles) and B. ionthados (triangles).

candida-complanata-foliata complex in which the bristles are not differentiated. Some species have differentiated bristles but none so marked or in such widely separated rows as *B. gabonensis. Barbatia sculpturata* Turton, 1932 is also much smaller and has only a few broad ribs on the posterior area, it is restricted to the sublittoral zone of the coasts of Natal and Cape Province (S. Africa) (KILBURN, 1983). Barbatia barbata (Linné, 1758) from the Mediterranean has a similar bristle pattern when small but later there is much less distinction between the primary and secondary bristles and in the largest specimens the whole of the dorsal area. Barbatia pistacia (Lamarck, 1819) from south eastern Australia has a similar rib pattern but the bristles are poorly differentiated and the rows of larger bristles are much more numerous.

## Barbatia ionthados n. sp.

(Pl. III, 7A-B; fig. 15; map 5)

TYPE MATERIAL : Holotype (20.6 mm), MNHN, South of Bassam, Côte d'Ivoire, 200 m, leg. MARCHE-MARCHAD, 13.X.1960. Paratypes : MNHN, off Cape three Points, Ghana, 4°43,5' N/2°45,5' W, 100 m, 1 spm., trawled R/V "La Rafale", Guinean Trawling Survey II, Sta. 27/6, 20.III.1964; NMWZ, as previous, 1 spm.

TYPE LOCALITY : South of Bassam, Côte d'Ivoire.

— 318 —



FIG. 14-15. — 14: Internal view of right valve of *Barbatia gabonensis* n. sp. Gabon. 15: Internal view of right valve of *Barbatia ionthados* n. sp. Côte d'Ivoire. (Scales bars = 5 mm.)

#### DESCRIPTION

Shell to 21 mm in length, very fragile. Equivalve. A little compressed. Very inequilateral, beaks in the anterior fifth.

Outline elongate rectangular, length to height ratio 2.6-2.7 : 1, dorsal and ventral margins more or less parallel. Posterior area not expanded but rather long, posterior angle rounded but distinct, posterior margin oblique to broadly rounded, posterior ventral junction rounded. Median area lacking sinus, ventral margin more or less straight, byssal gape minute. Anterior margin broadly rounded. Dorsal margin long, more or less straight.

Dorsal area very narrow, slightly cleft, umbonal separation slight. Ligament situated entirely behind the beaks, chevrons narrow numbering up to 4.

Hinge plate long, narrow; teeth in two series, separated by a very small gap at a point below the beaks; anterior set up to 9 teeth, posterior set up to 31 teeth. Teeth small, more or less straight, finely serrated; central teeth more or less vertical, lateral teeth slightly oblique.

Sculpture very fine, of weakly nodulose radial riblets, 88-96 in number but those on the anterior margin are difficult to distinguish and some shells may have more riblets. The riblets show no pattern except that they become progressively finer towards the anterior.

Periostracum of long very fine dark straw coloured suberect bristles which are longest on the posterior angle and most erect on the posterior slope. There is no trace of inter bristle lamellae.

Shell uniformly white.

Inner margin weakly serrate corresponding to radial riblets. Adductor scars subequal, posterior pedal/byssus retractor narrowly elongate. Byssus a thin narrow strap.

Length (mm)	Height (mm)	Tumidity (mm)	Anterior margin to beak (mm)	Rib No.
20.6	9.7	7.5	4.0	88
19.1	9.3	7.3	3.8	96
11.1	5.6	4.2	2.1	90

#### SELECTED SHELL MEASUREMENTS

DISTRIBUTION : Living specimens have been taken only off the northern coast of the Gulf of Guinea. A number of worn valves from off Senegal suggests a wider distribution and one might expect this species to occur throughout tropical West Africa.

MATERIAL EXAMINED : The type material; Senegal : off Gorée, 80 m, 8 v., poorly preserved, dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 20.II.1956, MNHN.

BIOTOPE : From the limited material available *B. ionthados* is apparently a deep water species living from 100-200 m. The functional byssus and general shell form suggest that it is epibyssate living attached to hard substrates. As with its Indo-Pacific counterpart *Barbatia tenella* Reeve, 1844 it may live in crevices or under stones where there is shelter but in the deep waters preferred by *B. ionthados* such protection may not be required.

DERIVATIO NOMINIS : *ionthados*, Greek, "long haired" or "shaggy", referring to the form of the periostracum.

REMARKS : Only one other species resembles *B. ionthados*, that is *B. tenella* Reeve, from the Indo-Pacific which shares the fragile shell, posterior ligament, fine sculpture and an entirely spicate periostracum. DALL, BARTSCH and REHDER (1938) erected the genus *Barbarca* and IREDALE (1939) the genus *Opularca*, for species close to this form. As they are clearly linked to *Barbatia* they would only warrant subgeneric status of which the earliest name is *Barbarca*.

> Barbatia legumen (Lamy, 1907) (Pl. III, 8, 9A-B, 10; fig. 16-18; map 6)

Arca legumen Lamy, 1907 : 74-76, pl. 1, fig. 3-4.

TYPE MATERIAL: MNHN, 16 syntypes from three different localities: 5 spm. Gabon, coll. DIBOWSKY, 1893; 5 spm., no locality, coll. LARGENTIÈRE, 1887; 2 spm., 4 v., "Bata Congo" (= Bata in Equatorial Guinea), coll. POBEGUIN, 1891. Among the latter lot is the specimen figured by LAMY (1907) and this is here selected as the lectotype.

TYPE LOCALITY : Bata, Equatorial Guinea. On the original label of the POBEGUIN collection this locality is always cited as "Bata Congo", at that time it belonged to the French Congo and did not become Spanish until 1900.

## DESCRIPTION

Shell to 52 mm in length. Equivalve. Compressed. Inequilateral, beaks in the anterior third.

Outline of adult submytiliform, often arcuate, anterior part narrow, posterior part expanded. Posterior area small; posterior angle broad, rounded and forming greater part of the posterior half of the shell; posterior margin long, oblique, sloping steeply, dorsal auricule indistinct or lacking. Median area distinctly sinuate, ventral margin long, arcuate. Anterior area small, demarcated by a rounded anterior angle; anterior margin narrowly rounded. Dorsal margin moderately long, straight. Outline of juveniles similar but posterior margin shorter and distinctly auriculate, ventral margin less arcuate and anterior area larger but anterior angle indistinct. The increasing arcuate development with age is illustrated in figure 17.

Dorsal area very narrow, deeply cleft; umbonal separation slight, ligament barely visible in joined valves. Ligament filling the whole of the dorsal area including the anterior part; ligament almost entirely lamellar, chevrons very strong numbering up to 5.

Hinge plate moderately thick; teeth probably in two series but the central teeth are usually worn giving the appearance of distinct anterior and posterior sets. When well preserved up to 50 teeth in all. Teeth slightly chevron shaped, finely serrated, becoming oblique laterally.

Sculpture of very numerous radial riblets, usually worn but best preserved in median sinus.

Periostracum initially with broad appressed bristles on posterior angle but later consisting primarily of thick concentric lamellar layers with scarcely emergent bristles. Colour a deep tanned dark brown.

Shell external colour white to cream, internally bluish in juveniles white in adults.

Adductor muscle scars unequal, the posterior twice the size of the anterior. Posterior pedal/byssus retractor small, narrowly oval.

## SELECTED SHELL MEASUREMENTS : See figure 16.

DISTRIBUTION : *Barbatia legumen* occurs only in the southern part of tropical West Africa, from Equatorial Guinea to southern Angola (Santo Antonio). The greater part of this range lies within the influence of the cold Benguela Current which in the southern winter can reach the coast of Gabon. Here and in Equatorial Guinea it seems to be very rare.

MATERIAL EXAMINED : The type material; **R.P. Congo** : Pointe Indienne, rocky shore 1 sh.; Pointe-Noire, Plage Sauvage, on beach, 3 v.; Plage Mondaine, on beach, numerous sh. and v.; off Plage ORSTOM, 3-7 m, numerous sh. and v., all leg. VON COSEL, XI-XII.1985; several sh. and v., leg. CROSNIER (Office Pte.-Noire); all MNHN. Angola : 10 km S of Ambrizete, Zaire province, intertidal, on beach, many fresh sh. and v.; Barra do Dande, Bengo province, between rocks at low tide, 2 spm.; Baia São Tiago, Bengo province, between rocks at low tide, 4 spm.; Cacuaco, Bengo province, between rocks, 0-1 m, 14 spm.; Corimba, Luanda province, Praia Etambar, between rocks at low tide, 5 spm., 1 sh.; Cabo Ledo, Luanda province, 10 m, 11 juv. spm., 3 juv. sh.; Santo Antonio, Benguela province, between rocks at low tide, 1 spm.; Baia das Pipas, Moçâmedes province, on rock platform, 1 juv. spm.; Porto Alexandre, Moçâmedes province, 2 m, 1 juv. v., all leg. GoFAS, 1982-85; all MNHN.

BIOTOPE : This species lives byssally attached to rocks, on the undersides of stones and to secondary hard substrates on soft sediments. The bathymetric range is from the intertidal to 1-2 m in the sublittoral.



FIG. 16-17. — 16: Box plots of the ratios of Total Shell Length to Height (L/H), Posterior Height (L/PH), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia legumen* from West Africa. 17: Graph of the ratio Total Shell Length : Difference in Median and Anterior Height plotted against Total Shell Length on log axis, showing the increasing arcuate form of the shell with age in *Barbatia legumen*.

## Remarks

Barbatia legumen belongs to a group of species which are submytiliform in shape and are typical inhabitants of the littoral and shallow sublittoral throughout the Indo-Pacific. The most widespread of these related species are *B. obliquata* (Gray, 1837) [Indian Ocean] and *B.* virescens (Reeve, 1844) [Indo-West Pacific]. *B. obliquata* is more expanded posteriorly, not auriculate and the ligament is restricted to behind the beaks. *B. virescens* can be auriculate and the ligament is on both sides of the beaks but the outline is much shorter, the sculpture more pronounced and the periostracum more spicate.

Some submytiliform species have been given generic rank; Savignyarca Jousseaume, 1898 (type S. savignyarca = Barbatia obliquata); Obliquarca Sacco, 1898 (type, Arca modiliformis Deshayes, 1831) and Barbatirus Iredale, 1939 (type B. minulus Iredale, 1939). HABE (1977) regards these as synonyms of Savignyarca but this presupposes that the submytiliform species have a common ancestry. We do not regard the common adaptive form as sufficient evidence to conclude monophyly because the incidence of convergent radiations within the Arcoidea is

— 322 —

well documented (STANLEY, 1972). In recent forms the convergent radiations within the Arcidae and Noetiidae illustrate the point.



FIG. 18. -- Internal view of right valve of Barbatia legumen Lamy. Angola. (Scale bar = 10 mm.)

## Subgenus NIPPONARCA Habe, 1951

It has not been our intention to introduce subgenera within *Barbatia* but in this case we have both anatomical and shell characters which allow us to confirm that *Nipponarca* is a useful division.

TYPE SPECIES : Arca bistrigata Dunker, 1858 : 87, pl. 30, fig. 4, see also HABE, 1951, fig. 49.

REVISED DIAGNOSIS : Shells to 50 mm. Equivalve. A little compressed. Inequilateral, beaks in the anterior third. Outline subrectangular, distinctly longer than high, dorsal and ventral margins subparallel. Hinge plate long, straight, teeth small. Dorsal area flat or almost so. Sculpture of few radial ribs; posterior ribs rather broad, flat and weakly sculptured; median ribs bifurcate, nodulose. Periostracum with long semi-erect bristles arising from the interspaces of the posterior angle. Labial palps very large with numerous sorting ridges. Byssate species inhabiting inshore areas where the conditions are turbid and often under estuarine influences.

SPECIES INCLUDED : Barbatia (Nipponarca) bistrigata (Dunker, 1858) [Indo-Pacific, Pakistan to Japan]. Barbatia (Nipponarca) allocostata this paper [tropical west Africa, Senegal to Sierra Leone]. Probably Barbatia signata (Dunker, 1858) [Indo-Pacific, India to China].

## Barbatia (Nipponarca) allocostata n. sp.

(Pl. IV, 1A-B, 2; fig. 19, 20; map 6)

TYPE MATERIAL : Holotype (28.4 mm), MNHN, Mouth of Rio Geba, Guinea-Bissau, 11°57,5' N/16°27' W, 7 m, agglomerations of live and dead *Crassostrea gasar*, on oyster shells, trawled R/V "André Nizery", leg. VON COSEL, 9.X.1988. Paratypes as holotype; MNHN, 9 spm.; NMWZ, 1990.017, 5 spm.

TYPE LOCALITY : Mouth of Rio Geba, 11°57,5' N/16°27'W, Guinea-Bissau.

## DESCRIPTION

Shell to 35 mm in length. Equivalve. A little compressed, most inflated across the anterior umbonal region and narrowing posteriorly. Inequilateral, beaks in the anterior third.

Outline subrectangular, much longer than high. Posterior area long, weakly demarcated, posterior angle rounded and becoming obsolete; posterior margin initially rounded, more or less vertical becoming oblique and some auriculate; posterior ventral junction rounded. Median area sulcate, ventral margin more or less straight, usually indented at byssal gape which is relatively short and narrow. Anterior area short, demarcated by weak anterior ridge; anterior margin broadly rounded. Dorsal margin long, straight.



FIG. 19-20. — 19 : Barbatia (Nipponarca) allocostata n. sp. A, internal view of right valve; B, external view of left valve with periostracum removed. Guinea-Bissau. 20 : Size series of dorsal views of Barbatia (Nipponarca) allocostata n. sp. Guinea-Bissau. (Scales bars = 5 mm.)

Dorsal area narrow, weakly cleft to flat, umbos well separated. Ligament initially behind the beaks but developing anteriorly in larger specimens; chevrons few, numbering up to 3.

Hinge plate narrow, teeth in two series but separation is indistinct, total number 50. Teeth small, weakly serrated, more or less straight, vertical centrally becoming a little oblique laterally.

Sculpture of relatively few, 26-28, radial ribs. Posterior 10-12 ribs broad, flat, more or less smooth; median ribs deeply bifurcate, nodulose; anterior ribs simple, irregularly nodulose.

Periostracum of very long semierect bristles arising from the rib interspaces over the posterior angle, elsewhere the pattern is the same but the bristles are much shorter and fragile. Bristles dark brown, remainder paler.

Shell mostly white but externally umbos grey and some with brown blotches on the posterior area; internally the umbonal cavity is suffused with green or greyish green tints.

Adductor muscle scars unequal, the posterior half as big again as anterior scar. Posterior pedal/byssus retractor scar narrowly elongate.

Anatomy (the following account is based on preserved specimens only)

The mantle edge (fig. 21) is entirely unfused and thickened posteriorly where it is thrown into small folds. Pigmentation is weak with only a few brown patches on the exterior of the outer fold in the posterior ventral region. Eyespots are absent but there is a single anterior dorsal pigment spot.

The gills (fig. 21) are typically arcoid and the gill axis is contorted suggesting that it is muscular and capable of extending the gills to the margin of the shell. The labial palps (fig. 21) are very large, semicircular in outline and with about 90 sorting ridges. These palps are very large for the genus, most being narrow with about 15-20 ridges.



FIG. 21. — Gross anatomy of *Barbatia (Nipponarca) allocostata* n. sp. viewed from the left side after removal of the left valve and mantle. (Scale bar = 5 mm.)

AA, anterior adductor muscle; B, byssus; CT, ctenidium; F, foot; LP, labial palps; ME, folded mantle edge; MEP, mantle edge pigmentation; PA, posterior adductor muscle; PPR, posterior pedal retractor muscle.

The gut is typical of the genus with a short oesophagus entering the stomach on its anterior dorsal face; the mid gut exits from the ventral floor of the stomach and passes deeply into the foot where it is weakly folded before forming a large anterior loop, then it passes dorsally across the right hand side of the stomach before bending posteriorly as the hind gut. The anterior loop is more prominent than in other species of *Barbatia*. The stomach is typically acroid but the food sorting area is restricted to the anterior dorsal food sorting caecum which is endowed with prominent sorting ridges. The right and anterior ventral

embayments have openings to the digestive diverticula and ridges are restricted to the rejection tract which follows the major typhlosole.

The foot (fig. 21) is large with a well developed heel and toe. The byssus groove is centrally placed and produces a relatively large but narrow sheet byssus (fig. 21) typical of the genus. The size of the byssus is reflected in the large posterior pedal/byssus retractor muscles which are narrowly elongate in section.

The anatomy of this species is similar in most ways to that of *Barbatia* as a whole in that it reflects an epibyssate habit. Significantly different is the size of the labial palps which are more typical of infaunal forms such as some *Anadara* species (HEATH, 1941 and LIM, 1966) and a new genus to be described in Part two of this revision. The biotope described below does appear to be one where resuspended matter is dense and this would explain the adaptive value of this epibyssate species having a large sorting capacity. A little surprisingly are the apparently weak mantle edge folds, these are usually more developed in species which inhabit muddy biotopes. The lack of pigmentation and eyespots on the mantle edge are not characteristics of *Barbatia* but again can be explained if the water column is so full of suspended matter that light is virtually excluded.

SELECTED SHELL MEASUREMENTS : See figure 22.

DISTRIBUTION : This species seems to have a limited distribution to the northern part of tropical West Africa. It is actually known from the extreme south of Senegal (southern Casamance) to the border between Guinea and Sierra Leone. Most probably it goes further south into Sierra Leone but we have never seen material from south of  $9^{\circ}$  N.



FIG. 22. — Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Barbatia (Nipponarca) allocostata* from West Africa.

MATERIAL EXAMINED : The type material; Senegal : Karabane Bôlon, Casamance, off Karabane, 4 m, 7 v.; Casamance, creek off Elinkine, 3 m. 3 v.; Ourong Bôlon, S-Casamance, 2-4 m, 2 v.; Cap Skirring-Diembéring, on beach, 1 v.; Essoukoudiak Bôlon, on the frontier to Guinea-Bissau, 4-6 m, coarse sand with pebbles, 1 spm., many v., all leg. von CoseL, 5-17.III.1988, all MNHN. Guinea-Bissau : Mouth of Rio Geba, 11°57,5' N/16°27' W, 7 m, on oysters (from type lot), 48 associated spm., MNHN. Guinea : Kaporo, NW coast of Conakry Peninsula, in front of ORSTOM, low tide, undersides of rocks, 1 spm.; Kaporo Port, Conakry Peninsula, rocks at low tide, 1 v.; Dixinn Port, NW coast of Conakry Peninsula, gravel, low tide, 1 v.; Conakry, Corniche Sud, in front of the "People's Palace", rocks at low tide, 4 v.; Kassa, Iles de Los, E-side, N of village, on the underside of a stone at low tide, 1 spm., all leg. von CosEL, V and XI.1988, all MNHN.



MAP 6. — Distribution of Barbatia legumen (circles) and B. allocostata (triangles).

BIOTOPE : Barbatia (Nipponarca) allocostata occurs on hard bottoms such as stones and rocks and is byssally attached. It is frequently found on offshore oyster beds consisting of Crassostrea gasar (Dautzenberg, 1891) where it is attached in crevices and between oyster shells. In Guinea-Bissau it was taken in trawls from sandy bottoms where it was found on shells of living Cymbium pepo (Lightfoot, 1786) which were also covered by small oysters. It was likewise found on living or hermit crab inhabited shells of Pugilina morio (L., 1858) and even on oyster covered valves of large bivalves like Macoma cancellata (Sowerby, 1873) and Mactra rostrata Spengler, 1802. B. allocostata seems to be limited to murky, sediment and seston laden water in regions with estuarine influences and seasonal salinity changes. On the rocky shores of the Conakry peninsula it was found on the sides and undersides of stones at low tide and is a rare but regular member of the Crassostrea gasar community. B. allocostata is not common in the intertidal and is most frequently found offshore to about 15 m.

DERIVATIO NOMINIS : *allocostata*, Greek, compounded from *allasso* meaning "to change" and *costatus* meaning "to bear ribs". This refers to the abrupt change in the form of the radial ribs from the median to posterior areas.

**REMARKS** : Barbatia (Nipponarca) allocostata is very closely allied to B. (N.) bistrigata (Dunker, 1858). The latter species is heavier shelled, reaches a larger size, the marginal crenulations are stronger, the anterior most, posterior ribs develop up to 4 ridges which do not bisect the rib and the posterior angle periostracal bristles are shorter and more stout.

## Genus BENTHARCA Thiele, 1931

TYPE SPECIES : Arca nodulosa Müller, 1776.

#### Bentharca asperula (Dall, 1881)

(Pl. VIII, 6A-B; fig. 23)

Macrodon asperula Dall, 1881 : 120-121. Arca profundicola Verril & Smith in VERRILL, 1885 : 439-440, pl. 44, fig. 23-23a. Arca (Barbatia) pteroessa Smith, 1885 : 844.

TYPE MATERIAL : IN USNM.

TYPE LOCALITY : Off S. E. United States, "Blake" sta. 33, 2875 m.

DESCRIPTION

Shell to 12 mm in length. Equivalve. Somewhat compressed. Inequilateral, beaks in the anterior quarter.

Outline subtrapezoidal. Anterior area greatly restricted, posterior roundly expanded giving an overall wedge-shaped appearance. Posterior margin broadly rounded; ventral margin sloping to narrow anterior margin, the latter slightly indented by byssal sinus. Median byssal sinus present at all sizes but byssal gape indistinct. Dorsal margin long and straight.

Dorsal area long, narrow initially but expanding rapidly with age. Ligament restricted to the posterior area but filling area between beaks with maturity.

Hinge plate very narrow; teeth in two series, separated by a wide edentulous gap. Teeth numbering up to five in each set; posterior teeth becoming subparallel to dorsal margin.

Sculpture very weak, of faint radial striae only. In other regions the sculpture can be a little stronger with faint raised riblets.

Periostracum usually worn and preserved at margins only; of very slender appressed bristles.

Colour white, periostracum a dirty olive brown.

Adductor muscle scars indistinct but unequal, the posterior about twice the size of the anterior. Byssus retractor muscle small, reflecting the weak byssus which consists of a single narrow strap.

DISTRIBUTION : A cosmopolitan species restricted to the abyssal zone from 2000-5000 m.

MATERIAL EXAMINED : Based on the data in OLIVER and ALLEN (1980).

BIOTOPE : Bentharca asperula lives attached to small stones, gravel and grit particles.

REMARKS : Two species of *Bentharca* occur in the Atlantic Ocean but the second *B.* nodulosa (Müller, 1776) has not yet been recorded from tropical West Africa. *B. nodulosa* lives
at shallow depths in the subarctic region and undergoes increasing submersion towards the south of its range reaching 3000 m off Madeira. It is a larger shell with a more coarse sculpture resembling that of the genus *Acar*.



FIG. 23. — Internal view of right valve and dorsal view of *Bentharca asperula* (Dall). Angola, 3975 m. (Scale bar = 2 mm.)

### Subfamily ANADARINAE

### Genus ANADARA Gray, 1847

### TYPE SPECIES : Arca antiquata Linné, 1758 (OD).

DIAGNOSIS : The generic systematics of most of the Anadarinae is presently confusing, especially concerning the distinction between *Anadara, Scapharca* and *Cunearca*. The distinctions as detailed by NEWELL in MOORE (1969) rest on the form of the ligament and on the equality of size of right and left valves. The ligament is referred to as amphidetic or opisthodetic, however in many species the ligament initially develops behind the beaks and eventually grows to fill the whole of the dorsal area. The degree of overlap of the right valve also has an ontogenetic relationship as well as being variable between species of obvious similarity in general form. These characters therefore are unreliable when used in isolation and NEWELL's definitions are consequently too broad. Other genera and subgenera have been revived or introduced mainly by OLSSON (1961) for panamic forms and by IREDALE (1939) for Australian forms. OLSSON (1961) uses a wider range of characters yet there is still reliance on some that do have ontogenetic changes and he does not compare his subgenera with those from the Indo-Pacific. Consequently a few divisions appear to be stable such as *Rasia* Gray, 1857; *Larkinia* Reinhart, 1935 and *Caloosarca* Olsson, 1961. In other cases such as OLSSON's (1961) use of *Diluvarca* Woodring, 1925 there remains a wide interpretation with some overlap into *Anadara* and *Scapharca* forms.

Our conclusion is to use *Anadara* as a broad generic group with subgeneric designations reserved for those cases where there is a clear resemblance in overall form to the type species of the subgenus concerned. There is clearly the need for a revised generic systematics on a world wide scale but this is beyond the scope of this paper and we refrain from introducing revised concepts in isolation.

# Anadara geissei (Dunker, 1891) (Pl. IV, 3A-B, 4A-B, 5, 6A-B; fig. 24; map 7)

Arca setigera Dunker, 1853 : 45, pl. 9, figs. 16-18 (non Reeve, 1844). Arca (Anomalocardia) dunkeri Kobelt, 1891 : 162, pl. 41, figs. 2-4. Arca (Anomalocardia) geissei Dunker in KOBELT, 1891 : 163-164, pl. 41, figs. 5-6.

TYPE MATERIAL : In SMF Frankfurt.

TYPE LOCALITY : Senegal.

### DESCRIPTION

Shell to 75 mm in length. Slightly inequivalve in juveniles but adults more or less equivalve. Not inflated, tumidity approximately 1/2 to 1/3 of the length. Inequilateral, beaks in the anterior third.



FIG. 24. — Internal view of right valve of Anadara geissei (Dunker). Angola. (Scale bar = 10 mm.)

Outline oblong, subrectangular, distinctly longer than high, juveniles distinctly expanded posteriorly, adults symmetrical. Posterior area indistinct; posterior angle marked in juveniles but becoming obsolete early in ontogeny; posterior margin obliquely subtruncate and slightly auriculate in juveniles, becoming simply subtruncate and finally rounded but more acute than anterior margin. Median area initially weakly sulcate, this noticeable to about 30 mm, then becoming progressively obsolete; ventral margin rather long and more or less straight, larger examples with a narrow anterior ventral byssus gape. Anterior margin broadly rounded. Dorsal margin rather long, straight.

Dorsal area long, rather narrow except in the largest specimens, umbonal separation moderate. Ligament initially opisthodetic but developing anteriorly at about 6 mm, apparently amphidetic by 15 mm and remaining with a single lateral chevron bordering a large fibrous sheet until about 40 mm when new chevrons are added these totalling 4-5 in the largest specimens.

Hinge plate rather narrow to moderate depending on the degree of encroachment by the ligament; teeth in two series, separation distinct, anterior set up to 30 teeth, posterior set up to 35 teeth. Teeth small, median series more or less straight and vertical; lateral series slightly chevron shaped, slightly oblique.

Sculpture of 29-32 radial ribs of which up to 18 anteriorly become progressively bifurcate, posterior ribs wider and more flat, anterior ribs very weakly ridged by low closely spaced cross bars.

Periostracum a thick coating of appressed laminae with bristles developing from the primary interspaces and from the bifurcate interspaces; anterior and median bristles short, lanceolate and soft, posterior bristles coarse, long, rigid, semi-erect; colour a deep reddish brown except for posterior bristles which are black; juveniles have a distinctive maculate pattern over the posterior area formed by differential thickening of the periostracum.



FIG. 25-26. -25: Box plots of the ratios of Total Shell Length to Heigth (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Anadara geissei* from West Africa (n = 27). 26: Bar chart of Rib Number for 22 shells of *Anadara geissei*.

## Shell white.

Adductor scars subequal, the posterior a little larger; posterior pedal/byssal retractor elongate oval. Inner margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See figure 25.

DISTRIBUTION : This species ranges from the Cape Verde Islands and Mauritania (Cap Blanc) to southern Angola (Benguela).

MATERIAL EXAMINED : Mauritania : Off Port Étienne, 20°20' N/16°22' W, 10 m, 3 v., coll. MARCHE-MARCHAD, 8.V.1965, MNHN. Cape Verde Islands : Sta. Lucia, 52 m, 1 spm. + 1 v., dredged R/V "Princess Alice" (sta. 1152), coll. H. FISCHER, 1901; off Boa Vista, 15m, 1 spm., dredged R/V "Calypso", 1959; SW of Boa Vista, 30 m, 2 v., 23.X.1948; São Vicente, Baia Porto Grande, beach, 11 v., leg. von Cosel, 19.XII.1978; São Vicente, Mindelo, beach, 3 v., leg. von Cosel, 17.XII.1978; all MNHN. Senegal: No precise locality, 1 spm., coll. VAYSSIÈRE; Rufisque, 18-20 m, many spm.; Pte. Cansado, 2 v.; W of Cap Rouge, 6 v., all coll. Mission GRUVEL, IV.1909; Gorée, 1 spm., coll. BAVAY; Gorée, 1 spm., coll. GERET; Cap Vert, 1 v., coll. MAURY; off Dakar, 50 m, 4 v.; Banc de Seminole, 43-45 m, 1 v.; off Gorée, 95-98 m, many v., all dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 1954-1956; Dakar, Anse Bernard, 1 spm., leg. MARCHE-MARCHAD; SE of Gorée, 14°41' N/17°23,2' W, 17 m, fine sand and mud, many v., dredged R/V "Louis Sauger", leg. VON COSEL, III.1988; M'Bour, Petite Côte, on beach, 1 v., leg. VON COSEL, 22.III. 1988; S. Casamance, Essoukoudiak Bôlon, 4-6 m, shelly sand, 1 v.; Karabane Bôlon, 3-4m, shelly sand, 1 v., both leg. VON COSEL, III.1988; N. Casamance, Abéné, 13°03'N/17°03'W, 20 m, very fine sand, 1 v.; Kafountine, 12°57,5' N/17°16,8' W, 35 m, medium sand and rocks, 1 v.;  $12^{\circ}56,9' \text{ N}/17^{\circ}06,8' \text{ W}, 22 \text{ m}, \text{ fine sand, } 3 \text{ v}.; 12^{\circ}44,5' \text{ N}/17^{\circ}27,3' \text{ W}, 40 \text{ m}, \text{ fine sand, } 8 \text{ v}.;$ 12°32' N/17°28,8' W, 45 m, fine sand, 3 v.; off Diembéring, 12°29,6' N/17°24,3' W, 35 m, fine sand, 1 v., all dredged R/V "Louis Sauger", leg. von Cosel, III.1988, all MNHN. Guinea-Bissau : Ilhas Bissagos, 7 v., leg. Mission GAIN, 1913, MNHN. Guinea : 10°30' N/15°43,5' W, 21 m, 2 v.; 10°12' N/13°06' W, 20 m, 2 spm.; 9°50' N/14°14'W, 15 m, 2 spm. + 5 v.; 9°30' N/13°53'W, 19 m, 1 spm.; 9°18' N/13°45' W, 21 m, 1 spm.; 9°12' N/14°15,1' W, 33 m, 1 spm.; 9°05,7' N/13°38' W, 24 m, 1 spm.; all dredged R/V "André Nizery", leg. von Cosel, IV-V.1988; 9°25' N/13°48,5' W, 1 v., dredged R/V "Président Théodore Tissier "; all MNHN. Sierra Leone : 7°15,5' N/12°51' W, 64 m, 1 v., dredged R/V "Calypso", leg. Marche-Marchad, 19.V.1956, MNHN. Nigeria : 4°00' N/6°11' E, 34m, 3 spm. ; 4°03' N/6°12' E, 32m. many v., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, both MNHN. Gabon: 0°14'S/9°14'E, 15-16 m, 2 v., dredged R/V "Thierry", Guinean Trawling Survey, leg. CHERBONNIER, 16.XI.1963, MNHN. R.P. Congo: Pointe-Noire, off plage ORSTOM, 3-7 m, 1 spm., 1 v.; plage ORSTOM, on beach, 1 v., plage Mondaine, on beach, 6 v., all leg. VON COSEL, XI-XII.1985; all MNHN. Angola : Baia de Corimba, Luanda province, 10-20 m, many spm.; Cacuaco, Bengo province, 5-10 m, many spm.; Ponta das Lagostas, 5-20 m, 1 spm.; Santo Antonio, Benguela province, intertidal, 1 v., all leg. GOFAS, 1981-85, all MNHN.

BIOTOPE : Anadara geissei inhabits fine and mixed sand with calcareous algae and shell debris. The juveniles are byssally attached to hard objects. It is a subtidal species ranging from 3-30 m.

## Remarks

This species was first described by DUNKER in 1853 as Arca setigera but that name is preoccupied by Arca setigera Reeve, 1844. KOBELT (1891 : 162) renamed this A. dunkeri but he also then described (1891 : 163-164) A. geissei using a manuscript name from DUNKER. The two are undoubtedly synonymous, A. geissei representing a young specimen and A. dunkeri an adult, but as the name A. geissei has been applied in all previous regional faunal studies we have retained this name.



FIG. 27. — Box plots for Length to Height ratios of three samples of *Anadara geissei* from Angola, Guinea and the Cape Verde Islands.



MAP 7. — Distribution of Anadara geissei.

Anadara geissei is not greatly variable throughout its range but the data displayed in figure 27 shows that there is variation in the Length/Height ratio, with some examples from the Cape Verde Islands being much higher and therefore more quadrate and in which the posterior margin remains subauriculate. The choice of samples used suggests clinal variation with latitude but it could also be ecophenotypic. The material and ecological data are limited

and at this time we consider all forms to be nothing more than individual varieties of A. geissei. It should be noted that the unusual specimens approach the Caribbean A. notabilis (Röding, 1798), and LOCARD (1898) and LAMY (1907) record, in our view erroneously, this species from Cape Verde Islands and Senegal.

We consider that A. geissei, A. floridana and the panamic species A. formosa (Sowerby, 1833) to be closely related and that the west African and Panamic species are most similar. The subgenus Rasia Gray, 1857 is probably a useful taxon within the Atlantic/Panamic provinces but we are not certain of its relationship with Indo-Pacific forms. A. geissei is a semi-infaunal species forming extensive beds reminiscent of *Modiolus* and it is consequently rather different from the truly infaunal burrowing forms of more typical Anadarinae. The type species of Anadara, A. antiquata is similar in being much longer than high and one of us has (OLIVER, pers. obs.) noted that this species is also semi-infaunal although to a lesser degree. It is therefore inappropriate at this time to make a decision on the value of the subgenus Rasia world wide.

## Anadara polii (Mayer, 1868)

(Pl. V, 1-9; fig. 30; map 8)

Arca antiquata Poli (non Linné, 1758), 1795 : 146, pl. 25, figs. 14-15.

Arca weinkauffi Crosse, 1862 : 324-325. Nomen dubium.

Arca diluvii auct. (non Lamarck, 1819 : 45).

Arca polii Mayer, 1868 : 75.

Arca diluvii var. inflato-subglobosa Aradas and Benoit, 1870 : 80.

Arca diluvii var. elongato-depressa Aradas and Benoit, 1870 : 80.

Arca (Anadara) sphaerica Kobelt, 1891 : 53-54, pl. 15, figs. 3-4.

- Arca talismani Locard, 1898 : 308, pl. 8, figs. 21-24. Arca polii var. minor Locard, 1898 : 305.
- Arca polii var. ventricosa Locard, 1898 : 305.

Arca polii var. transversa Locard, 1898 : 306.

Arca polii var. obligua Locard, 1898 : 306.

Arca polii var. angulosa Locard, 1898 : 306.

TYPE MATERIAL : The type material of Arca weinkauffi is uncertain : it was cited by CROSSE as being in the collection of WEINKAUFF, but later WEINKAUFF stated that it was never in his collection but was a single specimen in the Algerian Museum which had been stolen and replaced by a monstrosity of Arca diluvii (WEINKAUFF, 1880: 200). Given this uncertainty we regard A. weinkauffi as a nomen dubium.

Anadara polii was erected by MAYER in order to distinguish the recent Mediterranean species from the Miocene A. diluvii Lamarck, 1819. His name was based on figures of the recent species in a number of early publications of which the earliest is that of POLI, 1795. Consequently we regard the figure of A. antiquata Linné in POLI to be the type.

The holotype of A. sphaerica is in SMF Frankfurt but it bears no locality data.

The type material of the varieties inflato-subglobosa and elongato-depressa are cited as in the collection of ARADAS and BENOIT but its present location is not known.

The holotype of A. talismani is in MNHN and has a slightly broken hinge plate which has been misrepresented in the original figure in LOCARD (1898).

TYLE LOCALITY : Sicily.

Arca polii var. curta Locard, 1898 : 306.

### GENERAL DESCRIPTION

We have encountered great difficulty in assessing the significance of the large range of morphological variation seen within this taxon. Individual populations or samples show little variation but between samples the extremes can be such that it is difficult to imagine that they are part of a single taxon. More over there is no apparent pattern to this variation such that we are unable to definitely invoke clinal, bathymetric or ecological causes to explain it. This species is restricted to rather deep water and we have mostly small samples of live collected material with the larger samples of dead valves only. This restricts our ability to assess the distribution of the variants and also introduces the concern that some of the samples are of subfossil origin, notably that of the large shells from Senegal.

In conclusion we have refrained from separating the morphs into nominal taxa and instead we present a general diagnosis which highlights the common features and also individual descriptions of the morphs. With further collection it may be possible to explain this variation or even to conclude that this group is a complex of closely related species.

Shell to 55 mm in length. Rather heavy. Slightly inequivalve when small, more or less equivalve in adult, LV a-little larger. Inflated to greatly inflated, tumidity a little less than or a little greater than height. Inequilateral, beaks in the anterior 1/4 to 1/5. Outline oblong-subrectangular to suboval to ovate, usually longer than high but some only slightly so. Length/Height ratio varying from 1 : 1 to 1.3 : 1 (fig. 28). Posterior area weakly defined by rounded posterior angle; posterior margin oblique, curved to subtruncate. Median area deeply sulcate in post larval shell, otherwise rounded; ventral margin gently to deeply curved. Anterior area short to severely constricted. Length/Anterior to Beak Length varying from 2.9-4.7 (fig. 28); anterior margin broadly rounded.

Dorsal area moderately wide to wide. Ligament initially opisthodetic, developing anteriorly to fill dorsal area, chevrons widely spaced, few in number. Teeth numerous in two series.

Sculpture of 24-28 (these include the small anterior and posterior dorsal riblets when apparent) radial ribs (fig. 29), these rather narrow, high and equal to or narrower than interspaces except down posterior angle where they may be wider. Rib sculpture discrepant; LV with closely spaced, rather small raised cross bars, RV similar but much weaker.

Periostracum reddish brown, with bristles in the interspaces, these are all rather soft and fragile, anterior and median areas with short sharply pointed triangular bristles, posterior angle with very long, narrow, linear bristles.

#### MORPH DESCRIPTIONS

Anterior constricted morph (pl. V, 3B, 7, 8, 9) : Live collected shells to 25 mm. Inflated, tumidity only slightly less to slightly greater than height. Outline obliquely suboval, anteriorly constricted. Posterior margin oblique, gently curved, posterior ventral junction indistinct, rounded. Ventral margin curved, inclined towards the anterior and merging without a distinct junction into the broadly rounded anterior margin. Anterior area very small, sloping very steeply towards the umbo. Ligament extending anteriorly but not filling area completely.

Sculpture of 26-29, usually 27-28 ribs, all narrower than interspaces, noticeably steep sided and flat topped if not at all worn, LV sculpture delicate.



FIG. 28-29. — 28: Plots of Total Shell Length against Height and Anterior to Beak Length for 75 shells of *Anadara polii* from throughout its range. 29: Number of Ribs for 75 shells of *Anadara polii* from throught its range.

West African "subfossil" globose morph (pl. V, 3C, 4B) : Shells to 40 mm. Similar in outline to the above but some large shells are subspherical (probably gerontic). Sculpture of 24-28 ribs, usually 25-26 but this may be accounted for by wear of the posterior dorsal area. Ribs very noticeably narrower than interspaces. Ligament filling most of the dorsal area in large specimens.

**Oblong morph** (pl. V, 1A-B, 3A, 4A, 5, 6): Shells to 55 mm in length. Inflated but tumidity distinctly smaller than height. Outline oblong-subrectangular; posterior and anterior ventral junctions distinct, especially posterior; ventral margin more or less parallel to dorsal margin. Sculpture of 26-27 ribs, the posterior a little wider; rib sculpture on LV prominent especially on small shells.



FIG. 30. — Internal view of right valve and dorsal view of *Anadara polii* (Mayer). Anteriorly constricted morph from Cameroon. (Scale bar = 5 mm.)

DISTRIBUTION : This species is recorded from Portugal (Setubal), throughout the Mediterranean south to Angola (Moçâmedes).

MATERIAL EXAMINED : Mediterranean, Algeria : No precise details, 2 spm. + 1 v., MNHN. Italy : Sicily, Palermo, 1 spm., leg. MONTEROSATO, 1914; S. Andrea, 2 spm., leg. del Prête, 1928-1929, coll. Staadt; Circeo-Tirreno, leg. TITTONI, 2.1V.1957, coll. Staadt; Naples, 5 spm., coll. PETIT, 1873; Naples, 1 spm., old coll.; all MNHN. France : St. Raphaël, 1 spm., coll. LOCARD, 1892; off Banyuls-sur-Mer, 130-190 m, 9 spm.; both MNHN. Atlantic Morocco : between 37°01' N and 30°06' N, 20-180 m, numerous spm., sh. and v. from 25 dredging stations of R/V "Vanneau", 1923-1929; between 36°49' N and 33°43' N, 144-332 m, numerous sh. and v. from 6 stations of R/V "Cryos", BALGIM, VI.1984; all MNHN. Mauritania : SW of Nouakchott, 17°44' N/16°27' W, 100 m, 2 v., dredged "Leon Coursin", leg. MARCHE-MARCHAD, 3.II.1957, MNHN. Cape Verde Islands : S. Vicente, 1 v.; off São Tiago, 15°16,5' N/23°47,5' W, 50-65 m, 1 v.; 15°26,5' N/23°14' W, 100 m, 1 spm., all dredged R/V " Calypso", leg. MARCHE-MARCHAD, 1959; all MNHN. Senegal : Off Cap Vert, 14 v.; off Cap Vert 200-300 m, 1 v.; off Kayar, 110-120 m, 12 v., all leg. MARCHE-MARCHAD, 1967; 15°38' N/17°00' W, 130 m, 1 v., dredged "Léon Coursin", leg. MARCHE-MARCHAD, 1.II.1957; 14°50,1' N/17°29,3' W, 150 m, many v., dredged "Tenace", leg. MARCHE-MARCHAD, 15.III.1967; 14°23,5' N/17°24,5' W, 65-70 m, 1 spm. + 8 v.; off Dakar, 50 m, 1 spm.; 200 m, 1 spm.; 129-150 m, 9 v.; S of Gorée, 110-112 m, 13 v., all dredged R/V "Gérard Tréca", leg. MARCHE-MARCHAD, 1954-1958; Casamance, 12°32' N/28°8' W, 45m, fine sand, 2 v., dredged R/V "Louis Sauger", leg. von Cosel, 28.III.1988; 14°15,8' N/17°28' W, 100 m, leg. LEUNG TACK; Thiaroye, NNE of Dakar, 7-8m, leg. MARCHE-MARCHAD, 6.VI.1956; all MNHN. Liberia : 4°34,5' N/8°31' W, 64 m, 2 v.; 5°21,5' N/9°54,5' W, 73-80 m, 13 v., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, 20.V.1956, all MNHN. Côte d'Ivoire : Off Abidjan, 1 spm. + 9 v.; off Abidjan, 60 m, 1 spm.; off Abidjan, 70 m, 4 spm., all leg. LE LOEUFF (ORSTOM); off Abidjan, 2 v., leg. MARCHE-MARCHAD; 4°50' N/5°57' W, 70 m, 7 v.; 5°01' N/5°17' W, 40 m, 1 spm., both dredged R/V "La Rafale" Guinean Trawling Survey, IV.1964; all MNHN. Nigeria : 4°00' N/6°11' E, 2 v., dredged R/V "Calypso", MARCHE-MARCHAD, 1956, MNHN. Cameroon : 3°54,5' N/8°53' E, 62-64 m, mud, I spm.; leg. 3°54' N/8°50' E, 65-70 m, mud, 1 spm.; 2°51' N/9°41' E, 80 m, mud, 1 spm.; 2°39' N/9°40' E, 60-65 m, mud, 2 spm., all leg. CROSNIER, 22.VIII.1963; all MNHN. Gabon : Cap Lopez, on beach, 1 v., leg. CHEVALIER, 1984-1988; 0°32,8' S/8°43,1' E, 125-145 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. Angola : Off Ambrizete, Zaire province, 80 m, 4 v.; off Mussulo, Luanda province, 90-100 m, muddy ground, 12 v.; Ilha de Luanda, Luanda province, 120 m, many v.; Ilha de Luanda, 40-60 m, 2 v,; Ilha de Luanda, 90 m, 1 v.; Praia Amelia, Moçâmedes province, 40-60 m, 1 v., all leg. GoFAS, 1981-1984; all MNHN.

BIOTOPE : This species is restricted to offshore in depths from 50-200 m.



MAP 8. — Distribution of Anadara polii.

## Remarks

Of the morphs described the most common in tropical West Africa is the "anteriorly constricted" type. In West Africa living specimens are as yet all smaller than 25 mm which is half the size of those living in the Mediterranean. Considering the apparently subfossil samples the size ranges are more similar with a valve from Gabon reaching 40 mm. The most common type in the Mediterranean is the "oblong" morph but we have only 8 specimens and 1 valve from West Africa. Nowhere are the two extremes mutually exclusive and we cannot suggest that there is clinal variation. The globose morph represents many of the shells collected by the R/V "Vanneau" from off Morocco and is only rarely found in the Mediterranean. The large examples closely resemble the gerontic specimens of the subfossil samples from Senegal and

such specimens are the basis of both LOCARD'S A. talismani and probably KOBELT'S A. sphaerica.

The various morphs are shown to overlap in their distribution and there is a merging of one into the other when all samples are observed collectively. This degree of overlap can be seen in figures 31-32 which display the ranges of Length/Height and Length/Anterior/Beak Length ratios for shells from three parts of the range. These plots also show that the range of variation is greatest in the tropical West African shells. There is therefore no value in giving the morphs even varietal status and all are considered to be variants of *A. polii*.



FIG. 31-32. — 31 : Box plots of Shell Length to Height ratios of shells of Anadara polii from three parts of its range, Mediterranean, Morocco and tropical West Africa. 32 : Box plots of Length to Anterior to Beak Length of shells of Anadara polii from three parts of its range, Mediterranean, Morocco and tropical West Africa.

We have chosen to use the name A. polii Mayer for this species and not the more often used A. diluvii Lamarck. We do not consider that from our examination of the types of A. diluvii this species to be the Miocene/Pliocene counterpart of the Recent form because (i) the rib number is 33 not 24-28, (ii) the beaks are situated much more closely to the midpoint, (iii) the ribs are equal in width to the interspaces.

## Anadara eborensis n. sp. (Pl. VI, 1A-D; fig. 33; map 9)

TYPE MATERIAL : Holotype (31.9 mm), MNHN, off Grand Bassam, Côte d'Ivoire, 5°07' N/3°22' W, 20 m, dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 21.III.1964. Paratypes : MNHN, off Grand Lahou, Côte d'Ivoire, 5°00' N/5°28.5' W, 27 m, 1 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956; NMWZ, Guinea, 9°36' N/14°12' W, 21 m, 1 spm., dredged R/V "André Nizery", leg. von Cosel, 19.V.1988.

TYPE LOCALITY : Côte d'Ivoire, off Grand Bassam.

### DESCRIPTION

Shell to 32 mm in length. Heavy. Slightly inequivalve, LV a little larger. Inflated, almost as tumid as high, strongly umbonate. Inequilateral, beaks almost in the anterior quarter.

Outline subquadrate, only slightly longer than high. Posterior area broad sloping steeply, set off by strong but rounded posterior angle; posterior margin obliquely subtruncate, more or less straight; posterior ventral junction distinct, sharply rounded. Median area narrow, more or less flat except in very earliest stages in which it is deeply sulcate, ventral margin gently curved or more or less straight. Anterior margin broadly rounded. Dorsal margin straight, anterior junction almost 90°, posterior junction oblique.

Dorsal area broad, slightly cleft or more or less flat, umbonal separation wide. Ligament initially developing with a single posterior chevron, then adding anteriorly towards the beaks and eventually in front of the beaks but chevron number remaining low with up to 5 growth points on the hinge line, chevrons narrow.

Hinge plate moderately thick, teeth in two series, separation slight with posterior set pushing over the anterior, anterior set up to 24 teeth, posterior set up to 27 teeth. Teeth laminar, narrow, vertical.

Sculpture of 24-27 (usually 25) radial ribs, these narrow and only half the width of the interspaces, steeply angled with narrower, rather flat top; RV weakly nodulose, LV almost smooth.

Periostracum rust brown with slightly darker, short, thorn like, recurving bristles arising from the interspaces of the anterior and median areas; those on the posterior angle all worn.

Shell white.

Adductor muscle scars unequal, the posterior considerably larger. Internal margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See in Remarks section under Anadara subglobosa.

DISTRIBUTION : This species has a restricted distribution from Guinea to Côte d'Ivoire and Gabon.

MATERIAL EXAMINED : The type material; Guinea :  $9^{\circ}40' \text{ N}/14^{\circ}05' \text{ W}$ , 18 m, many v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956;  $9^{\circ}12' \text{ N}/13^{\circ}43,5' \text{ W}$ , 24 m, 1 spm.;  $9^{\circ}01' \text{ N}/13^{\circ}30' \text{ W}$ , 12 m, 1 spm., both dredged R/V "André Nizery", leg. von Cosel, 27.IX.1988; all MNHN. Liberia :

 $4^{\circ}34,5' N/8^{\circ}31'W$ , 64 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. Côte d'Ivoire :  $5^{\circ}03' N/5^{\circ}25'W$ , 20-25 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 21.V.1956; off Abidjan, 2 spm., dredged R/V "Reine Pokou", leg. Le LOEUFF (ORSTOM); both MNHN. Nigeria :  $4^{\circ}34,5' N/8^{\circ}31'E$ , 64 m, 1 v.;  $4^{\circ}03' N/6^{\circ}12'E$ , 32 m, 1 v., both dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. Gabon : Cap Lopez, 3 v., leg. CHEVALIER, 1984-1988, MNHN.



MAP 9. — Distribution of Anadara eborensis.

BIOTOPE : This species has been dredged from mud and mixed muddy substrates offshores from 18 to 64 m.

DERIVATIO NOMINIS : *eborensis*, Latin, derived from *eboris*, "ivory" with the suffix *ensis* denoting place referring to the type locality of the Côte d'Ivoire.

REMARKS : The heavy subquadrate appearance of this shell is reminiscent of other species placed in the subgenus *Larkinia* but those species have a true amphidetic ligament. The only Caribbean species with any similarity is *Anadara brasiliana* but it also has a truly amphidetic ligament, the ribs are as broad as the interspaces and the rib sculpture is more prominent. Most akin to *A. eborensis* is perhaps *A. (Esmerarca) reinharti* Lowe, 1935, both in the general shape, the form of the ligament and the weak discrepant rib sculpture. The posterior margin of *A. reinharti* by comparison is rounded, there is a slight posterior ventral sinuation and the ribs are as wide or wider than the interspaces.



FIG. 33. — Internal view of right valve and dorsal view of Anadara eborensis n. sp. Côte d'Ivoire. (Scale bar = 5 mm.)

# Anadara subglobosa (Dunker, 1891) (Pl. VI, 2A-B; fig. 34; map 10)

Arca (Anomalocardia) subglobosa Dunker in KOBELT, 1891 : 99, pl. 26, figs 7-8.

TYPE MATERIAL : Most probably in ZMB Berlin. In the MNHN we have located a single specimen in the BAVAY collection which is marked as coming from VON MALTZAN, collected at Gorée, Senegal. This agrees with the data available with the type as cited by DUNKER and also agrees with his figure (1891 : pl. 26, fi.g. 8).

TYPE LOCALITY : Gorée, Senegal.

### DESCRIPTION

Shell to 19 mm in length. Slightly inequivalve in juveniles, more or less equivalve in adults. Inflated to strongly inflated, usually with tumidity less than height but some adults with tumidity greater than height, umbonate but not greatly. Inequilateral, beaks in the anterior 1/3 to 1/4.

Outline subrectangular, adults always distinctly longer than high with the anterior half of the shell a little more expanded than the posterior, juveniles less so. Posterior area relatively short, sloping rather steeply and demarcated by a distinct, acutely rounded posterior angle but this is not so marked in the juveniles; posterior margin oblique, moderately long, more or less straight; posterior ventral junction distinct, roundly acute. Median area strongly sulcate in post larval shell and to a lesser degree in juveniles to about 8 mm, otherwise gently curved; ventral margin gently curved, subparallel to dorsal margin. Anterior area small, anterior margin broadly rounded, anterior ventral junction obsolete. Dorsal margin straight.

Dorsal area rather wide, more so anterior to the beaks, umbonal separation moderate to wide. Ligament initially opisthodetic but very rapidly developing anteriorly and appearing

- 342 —

secondarily amphidetic except for a small anterior ligament free area; chevrons very few, 2-3 in number, very narrow.



FIG. 34. — Internal view of right valve and dorsal view of *Anadara subglobosa* (Dunker). Mauritania. (Scale bar = 5 mm.)

Hinge plate moderately thick; teeth in 2 series, the anterior set pushing below the posterior at their junction; anterior set up to 18 teeth, posterior set up to 24 teeth. Teeth laminar, all teeth vertical except for a few slightly oblique posterior marginals.

Sculpture of 28-31 radial ribs, these narrower than interspaces in adults with steeply angled sides and a rather flat topped appearance. Rib sculpture discrepant, stronger on LV of rather long, sparse nodules, RV more or less smooth except for weak nodules on anterior ribs. Interspace sculpture distinct of widely spaced concentric, crescentric notches.

Periostracum rarely preserved in a good state; generally rust brown in colour with sparse bristles in the interspaces; anterior and median bristles thorn-like recurved dorsally; on posterior angle longer, narrower.

Shell white.

Adductor scars unequal, the posterior twice the size of anterior, posterior quadrate; anterior rounded, often a little raised. Inner margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See below in Remarks section.

DISTRIBUTION : From Mauritania (17°N) south to Côte d'Ivoire.

MATERIAL EXAMINED : **Mauritania** :  $17^{\circ}30' \text{ N}/16^{\circ}15' \text{ W}$ , 41 m, 1 spm., dredged R/V "N'Diago", leg. RICHER DE FORGES, 1981, MNHN. **Senegal** : Gorée, 1 spm., coll. BAVAY ex coll. VON MALTZAN; Gorée, 1 spm., coll. JOUSSEAUME; SE of Gorée,  $14^{\circ}41' \text{ N}/17^{\circ}23,2' \text{ W}$ , 17 m, fine sand and mud, 2 v., dredged R/V "Louis Sauger", leg. VON COSEL, 24.III.1988; S of Gorée, 65 m, many v.; 110-112 m, 1 v.; 95-98 m, many v.; SW of Cap Manuel, 50 m, 1 v., all dredged "Gérard Tréca", leg. MARCHE-MARCHAD, II.1954;  $14^{\circ}50' \text{ N}/17^{\circ}29' \text{ W}$ , 150 m, dredged "Tenace", leg. MARCHE-MARCHAD, 15.III.1967;  $14^{\circ}31,9' \text{ N}/17^{\circ}13,5' \text{ W}$ , 28 m, 1 spm., coll. LEUNG TACK, 1983-1984; Casamance, Abéné, 13°01,8' N/  $17^{\circ}25,5' \text{ W}$ , 53 m, hard ground and fine sand, 1 v.;  $12^{\circ}46,6' \text{ N}/17^{\circ}19,2' \text{ W}$ , 32 m, carbonate and fine sand, 1 v., all dredged R/V "Louis Sauger", leg. VON COSEL, 28-29.III.1988;  $14^{\circ}2,5' \text{ N}/17^{\circ}09,1' \text{ W}$ , 24 m, 2 v., dredged "Cdt. Henri Gomis", leg. BODARD, 7.XII.1966;  $13^{\circ}01' \text{ N}/17^{\circ}24' \text{ W}$ , 51-55 m, 1 spm. + 2 v., dredged, R/V "Calypso", leg. MARCHE-MARCHAD, 1956; all MNHN. **Ghana** :  $4^{\circ}57' \text{ N}/2^{\circ}42' \text{ W}$ , 40 m, muddy ground, 1 spm. + 1 v., dredged R/V "La Rafale" Guinean Trawling Survey, leg. CHERBONNIER, 19.III.1964; MNHN. Côte d'Ivoire :  $4^{\circ}52,5' \text{ N}/5^{\circ}57,5' \text{ W}$ , 40 m, hard ground and calcareous algae, 2 v.;  $5^{\circ}05' \text{ N}/3^{\circ}22' \text{ W}$ , 30 m, mud, sand and shell gravel, 2 spm. + 4 v.;  $5^{\circ}07' \text{ N}/3^{\circ}22' \text{ W}$ , 20 m, 1 spm.; all dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, III and IV.1964; all MNHN.

BIOTOPE : This species has been collected primarily in deep water from 17-200 m.

## Remarks

This species is clearly related to *Anadara eborensis* (this paper) by the similarity in growth of the ligament and the shape and sculpture of the radial ribs. It differs from that species in being rectangular rather than quadrate, that is with a larger Length/Height ratio (fig. 35); and also less tumid (fig. 35).

Although there is a degree of overlap with these characters the rib number is consistently different between the two species *A. subglobosa* having more ribs, 28-31 as against 24-27 for *A. eborensis* (fig. 36).



MAP 10. - Distribution of Anadara subglobosa (circles) and A. camerunensis (triangles).

The distribution of these species overlap, and we have not found intermediate samples in the material at hand. It is of interest to note that it does seem possible to distinguish non overlapping morphologics in some groups yet not in others. The degree of plasticity in shell form within the *Anadara* group has never been explained but is well illustrated by referring to any of the major works on the Tertiary faunas of Europe or the Caribbean where a multitude of forms are described. Until we have understanding of this plasticity the species systematics will remain fraught with difficulty so long as we are limited to traditional conchological methods. With the Recent fauna recourse to electrophoretic and genetic methodology could be advantageous.



FIG. 35-36. — 35 : Box plots of Length to Height and Length to Tumidity ratios for *Anadara eborensis* (n = 14) and *A. subglobosa* (n = 20). 36 : Bar chart of rib number in *Anadara eborensis* (mode 25) and *A. subglobosa* (mode 31).

Anadara senegalensis (Gmelin, 1791) (Pl. VI, 3A-D, 4A-B, 5A-B; pl. VII, 1-4; fig. 39; map 11)

"Le Robet" Adanson, 1757 : pl. 248, fig. 6. Arca senegalensis Gmelin, 1791 : 3312. Arca pertusa Reeve, 1844 : Sp. 28, pl. V.

TYPE MATERIAL : Lectotype (here selected), MNHN, from coll. ADANSON, a left valve, 20 mm in length. This is not the valve cited by FISCHER-PIETTE (1942) as the figured specimen in ADANSON (1757) but we argue that the original figure is so poor that it does not adequately represent any of the specimens labelled by ADANSON as "Le Robet". Furthermore the two valves cited by FISCHER-PIETTE are not a pair,

the right valve does not fit into the left valve and the widths of the dorsal areas are different. Paralectotype as lectotype, 2 valves.

TYPE LOCALITY : Senegal.

## DESCRIPTION

Shell to 25 mm in length. Inequivalve, LV larger than RV. Greatly inflated, tumidity almost equal to or a little greater than height; strongly umbonate. Inequilateral, beaks in the anterior third.

Outline rhomboidal-oval, initially a little longer than high, later almost as high as long. Posterior area very short and very steep; posterior angle distinct but rounded; posterior margin long, a little oblique, almost vertical, gently curving in juveniles but with a subtle angulation in adults. Median area curved except in post larval shells which are sulcate; ventral margin curved, posterior ventral junction slightly angulate, anterior ventral junction not marked but curving into anterior margin which is short, weakly curved and almost vertical. Dorsal margin straight, rather short.

Dorsal area slightly cleft, rather narrow, umbonal separation slight. Ligament initially opisthodetic, later apparently amphidetic but with a somewhat larger anterior ligament free area, chevrons widely spaced, numbering up to 4.

Hinge plate thick, teeth in two series, separation slight, anterior set up to 22 teeth, posterior to 20 teeth. Teeth laminar, some weakly chevron shaped, all more or less vertical.

Sculpture discrepant, of 23-24 radial ribs, LV with anterior 15-16 ribs strongly nodulose formed by thickened crossbars, RV with anterior 6-10 ribs more weakly nodulose.

Periostracum a thin rust brown coating except for spicate bristles arising from interspaces, on posterior area of closely spaced, thin, long, black, erect bristles; on median area of shorter wider bristles directed posteriorly.

Shell white.

Adductor scars unequal, posterior twice as large as anterior, pedal retractor scars small indistinct. Inner margin strongly crenulate corresponding to radial sculpture.

SELECTED SHELL MEASUREMENTS : See figure 37.

**Casamance variety** (pl. VII, 3-4) : This larger (to 29 mm) variant differs from the typical form in being distinctly longer than high and is therefore oblong-rhomboidal in outline. The sculpture is slightly weaker but the nodules are still large if not so raised. The shell is thinner and consequently the hinge plate is weaker and the teeth smaller. This is the form represented by ADANSON's type specimens.

DISTRIBUTION : This species has been recorded from Guinea south to Angola (Bengo province).

MATERIAL EXAMINED : Senegal : No precise locality, 4 spm., coll. H. FISCHER; Dakar, 2 v., coll. CHEVALIER, 1900; N. Casamance, Kafountine, beach to the south, 4 v., Abéné-Kafountine, beach, many v.; S. Casamance, Cap Skirring-Diembéring, on beach, many v.; Cap Skirring, beach to the south, many v.; Bôlon opposite Elinkine, 3 m, 8 v.; off Kafountine, 3-6 m, 1 v.; Katakalous Bôlon, 2-4 m, 1 v.; S of Cap Skirring, 3-5 m, many v., all leg. von CosEL, 5-17.III.1988; off Cap Skirring, 12°22,5' N/17°03' W,

20 m, 2 v.; off Cap Skirring, 12°23' N/16°52,8' W, 13 m, 5 v.; 12°46,9' N/17°29,9' W, 45 m, many spm., all dredged R/V "Louis Sauger", leg. von Cosel, 27-29.III.1988, all MNHN. Guinea-Bissau : Casamance border, Essoukoudiak Bôlon, 5-6 m, 2 v., leg. von Cosel, 7.III.1988; 11°58,5' N/16°59' W, 14 m, 3 spm.; 11°53' N/16°56,5' W, 11 m, 2 spm.; 12°05' N/17°02,5' W, 14 m, many spm., all dredged R/V "André Nizery", leg. von Cosel, 7.X.1988; all MNHN. Guinea : No precise locality, 2 spm., coll. PARFAIT, 1889; Cap Varella, 3 v., coll. MAUNY, 1964; Conakry, many v., coll. DUFOSSÉ, 1905; all MNHN. Côte d'Ivoire : Off Abidjan, 1 spm., leg. MARCHE-MARCHAD; Sassandra, Batebré beach, many v., coll. AUBERT DE LA RUE, 1950; off Abidjan, 4°50' N/5°57' W, 70 m, 8 v., dredged R/V "La Rafale", Guinean Trawling Survey, leg. CHERBONNIER, 4.IV.1964; off Bassam, 20 m, 1 spm.; Abidjan region, 20-26 m, 27 spm. + 1 sh. from 4 stations, all dredged R/V "Reine Pokou", leg. LE LOEUFF (ORSTOM), 1966-1967; all MNHN. Togo: Lomé, 14 v., MNHN. Gabon: No precise locality, 1 sh., coll. H. FISCHER; Cap Lopez, beach south of lighthouse point, 6 v., leg. CHEVALHER, 1984-1988, both MNHN. R.P. Congo: Off Conkouati, 4°00' S/10°59' E, 19m, many v.; 4°10' S/11°15' E, 19m, 1 spm., both trawled "Kounda", leg. VON COSEL, XII.1985; Pointe-Noire, Plage Mondaine, many v.; Plage Raffinerie, 6 v., Plage ORSTOM, 2 v.; Baie de Pointe Noire, off Plage ORSTOM, 5-7m, many spm., dredged from muddy fine sand; 3-4m, 5 spm. + many v., dredged from fine sand and gravel; off Plage Mondaine, 5m, 3 v., dredged from muddy fine sand; off Songolo, 5-6 m, 1 v., dredged from muddy fine sand, off Plage Raffinerie, 1 m, 3 v., all leg. VON COSEL, X-XII.1985; all MNHN. Angola: Cacuaco, Bengo province, 0-10m, 1 spm. + 5 sh. + 6 v.; Moçâmedes, Moçâmedes province, 0-2 m, 1 v.; Ponta do Mussulo, Luanda province, on beach, 1 v., all leg. GOFAS, 1981-1985, all MNHN.



FIG. 37-38. — 37 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of Anadara senegalensis typical form from Guinea-Bissau, Côte d'Ivoire and R.P. Congo (n = 59). 38 : Box plots of the ratios of Total Shell Length to Height and Tumidity of three samples of Anadara senegalensis from the Casamance region of West Africa (n = 20 per sample).

BIOTOPE : Live collected material of this species has been collected in shallow depths from the sublittoral to  $30 \,\text{m}$ .



MAP 11-12. — 11 : Distribution of Anadara senegalensis. 12 : Coast of Casamance with the localities of Anadara senegalensis. 1. Abéné; 2. Kafountine; 3. Diembéring; 4. Cap Skirring. Scale = 10 km.

## Remarks

This is the most frequently encountered *Anadara* in the West African material examined, and for most of its range it is well defined and not variable. There are, however, a number of samples principally from the Casamance district of Senegal but also some from the R.P. Congo and the northern provinces of Angola that include a rather different form. This form is described above as the Casamance variant.

We are fortunate to have a few large samples of beached valves from Casamance (map 12) and the Length/Height and Length/Tumidity ratios are plotted in figure 38. This shows that the sample (Abéné) from the northern part, close to the Gambia River, contains more "Casamance" variants than those from further south, south of the Casamance River, but that the two forms are not mutually exclusive. The fact that the « Casamance » variant is

also to be found around the Congo river indicates that this may not be clinal variation but is perhaps linked to environmental conditions close to the estuaries of large rivers. Much more detailed collecting would be needed to assess whether or not the "Casamance" variant is truly linked to these ecological conditions.

One factor ANOVA table for Length to Height ratios of three samples of Anadara senegalensis from the Casamance region.

Group	Count	Mean	Std. Dev
Dimbéring	30	1.149	.067
Cap Skirring	30	1.17	.086
Abéné	22	1.273	.095
Comparison	Mean Diff	Schoffe F-test	
Comparison	ivican Diff.	Scherre 1-test	
Diembéring vs Cap Skirring	021	. 51	
Diembéring vs Abéné	125	14.56*	
Cap Skirring vs Abéné	—.103	9.979*	

One factor ANOVA, 2 degrees of freedom, F = 15.934, p = .001.

\* Significant at 95 %.



FIG. 39. — Internal view of right valve and dorsal view of Anadara senegalensis (Gmelin). Typical adult shell from Côte d'Ivoire. (Scale bar = 5 mm.)

The ANOVA table for the Length to Height ratios shows a statistically significant difference between the Abéné sample (from the North) and those from Cap Skirring and Diembéring (from the South). However over the total range the Casamance variant and the typical form grade into each other. The use of such analyses for the separation of taxa can be misleading and in general for *Anadara* species other non continuous variables such as rib number should always be considered.

Anadara senegalensis would from its general form be considered to belong the subgenus Cunearca but it differs in the form of the ligament which has many chevrons and is secondarily amphidetic. The ligament of the type species of *Cunearca (Arca incongrua* Say, 1822) consists of an amphidetic sheet of fibrous ligament with a single outer lamellar chevron. This form of ligament is also found in *Anadara chemnitzi* Philippi, which is the closest Caribbean counterpart to *A. senegalensis*, and in *Anadara pilula*, a similar Indo-Pacific species. The significance of such differences in ligament structure have never been considered within the Anadariinae, and it is not known whether it should be given any phylogenetic credence.

## Anadara camerunensis n. sp.

(Pl. V, 6A-C; fig. 43; map 10)

TYPE MATERIAL : Holotype (15.1 mm), MNHN, Cameroon, Victoria (now Limbe)-Bota, 8-10 m, leg. VON COSEL, 4.XII.1985. Paratypes : as holotype, 3 spm.; NMWZ, Cameroon, Victoria-Bota, 5-6 m, leg. VON COSEL, 4.XII.1985, 2 spm.

TYPE LOCALITY : Cameroon, Victoria (now Limbe).

### DESCRIPTION

Shell to 16.4 mm in height. Inequivalve, LV larger than RV. Greatly inflated, tumidity almost as great as length; strongly umbonate. Inequilateral, beaks in the anterior third.

Outline obliquely-oval, subrhomboidal, higher than long. Posterior area short, very steeply sloping; posterior angle prominent but rounded; posterior margin very long, slightly oblique, very gently curved. Median area rounded except in post larval shells which are sulcate; ventral margin curving into anterior margin which is broadly rounded, posterior ventral junction roundly angulate. Dorsal margin straight.

Dorsal area slightly cleft, wider in front of beaks, umbonal separation moderate. Ligament initially opisthodetic, later apparently amphidetic but ligament free area a little large anteriorly, chevrons few, widely spaced, numbering up to 3.

Hinge plate thick, teeth in two series, separation indistinct, anterior set up to 17 teeth, posterior set up to 17 teeth. Teeth laminar or slightly chevron shaped, more or less vertical.

Sculpture of 21-22 radial ribs, discrepantly nodulose; RV with the anterior 9-11 ribs nodulose, LV with anterior 13-14 ribs strongly nodulose, all nodules as raised cross bars across whole of rib.

Periostracum a thin coating, dark rust brown in colour except for interspaces which bear erect bristles, on the posterior area these are very long rigid black hairs, elsewhere much shorter and wider.

# Shell white.

Adductor scars unequal, posterior twice the size of the anterior, pedal retractor scars indistinct. Inner margin deeply crenulate corresponding to radial ribs.

Selected shell measurements

Length (mm)	Height (mm)	Tumidity (mm)	Anterior to beak (mm)	Hinge line to ventral (mm)	Rib No.	Locality
15.1	16.4	14.9	5.4	12.3	[9/13] 21	Cameroon, 8-10 m
12.6	13.2	12.6	4.2	9.8	[11/14] 22	
12.4	13.2	11.7	4.0	10.3	[10/14] 22	
11.6	12.0	10.1	3.8	9.1	[10/14] 22	
11.1	12.7	11.3	3.9	9.7	21	Cameroon, 24 m
12.4	13.2	12.2	3.7	10.6	21	Cameroon, 5-6 m

(The numbers in square brackets mark the nodulose ribs in RV and LV.)



FIG. 40-41. — 40 : Box plots of Length to Height ratios for samples of Anadara senegalensis [Abéné (n = 20), Diembéring (n = 20), Abidjan (n = 20) and Congo (n = 23)] and A. camerunensis [Cameroon (n = 6)]. 41 : Graph of Length to Height ratios plotted against Shell Length for Anadara senegalensis (n = 130) and A. camerunensis (n = 6). Overlapping points are shown as increasing symbol sizes.

DISTRIBUTION : This species is restricted to the coast of Cameroon.

MATERIAL EXAMINED : Cameroon : Victoria/Limbe-Bota, 8-10 m, 5 v., leg. von CoseL; off Victoria, 3°44' N/9°11' E, 24 m, 1 spm; between Wouri estuary and Cap Nachtigal, 3°44' N/9°22' E, 13 m, 1 v., both trawled "Campo Star", leg. von CoseL, XII.1985; all MNHN.

BIOTOPE : This species is infaunal and inhabits muddy fine sand from 5 to 24m.

DERIVATIO NOMINIS : camerunensis after the Republic of Cameroon, the type locality.

### Remarks

We have considered at length that this species might be an ecomorph of *Anadara* senegalensis, however we can find no environmental parameters that would give rise to the changes observed. In *A. camerunensis* the adult size is only 16 mm as compared to 35 mm for *A. senegalensis*. For most of its ontogeny *A. camerunensis* is higher than long which is the case for only the occasional specimens of *A. senegalensis* (fig. 40-41).

The rib number, although not greatly different, is totally consistent : that of A. camerunensis from 21-22 and for A. senegalensis 23-24 (fig. 42).



FIG. 42. — Rib Number frequency data for Anadara senegalensis (n = 130) and A. camerunensis (n = 6) shown as percentile line plots.

Comparing the adults of each, *A. camerunensis* is more oblique, the posterior ventral margin being more attenuated. Overlaps with *A. senegalensis* have not yet been found, and we have consequently given this form specific status.

Anadara camerunensis has its closests counterpart in the Panamic province, A. nux (Sowerby, 1833), but differs in the form of the ligament. In A. nux there is a single outer chevron (fig. 43C) bounding a large median sheet, and the growth is amphidetic. This type of ligament is found in none of the West African Anadarinae included in this paper but is not uncommon in the Panamic, Caribbean and Indo-Pacific. The shape of the shell of A. nux and A. camerunensis would place them in Cunearca. However, should the adaptive form of the shell

be given greater phyletic weight than the form of the ligament? This problem requires a complete cladistic analysis of the Anadarinae and highlights the inconsistency in the current generic systematics.



FIG. 43. — A-B, Internal view of right valve and dorsal view of *Anadara camerunensis* n. sp. Cameroon; C, Dorsal view of *Anadara nux* (Sowerby). Ecuador. (Scale bar = 3 mm.)

Anadara corbuloides (Monterosato, 1878) (Pl. VII, 5A-D; fig. 46; map 12)

Arca corbuloides Monterosato, 1878 : 67.

TYPE MATERIAL : Not located.

TYPE LOCALITY : Algeria.

### DESCRIPTION

Shell to 70 mm in length. Inequivalve, LV larger than RV, most noticeable in small specimens, obsolete in the larger examples. Inflated, tumidity normally a little greater than half the length but in gerontic specimens much greater. Inequilateral, beaks in the anterior half.

Outline subelliptical, longer than high. Posterior area poorly defined; posterior angle rapidly becoming obsolete; posterior margin evenly rounded except for a small indentation at the posterior dorsal junction. Median area rounded but sulcate in post larval shell; ventral margin curved lacking angles with anterior and posterior margins. Anterior margin broadly rounded to obliquely curved, some becoming rather straight resulting in a subacute anterior dorsal junction. Dorsal margin relatively long, straight.

Dorsal area becoming wide, slightly cleft, umbonal separation moderate. Ligament initially opisthodetic becoming secondarily amphidetic; chevrons few, widely separated, numbering up to 5.

Hinge plate rather narrow, teeth in two series, separation indistinct, anterior set up to

37 teeth, posterior to 39 teeth. Teeth small, pointed, larger teeth slightly chevron shaped, most vertical, a few lateral teeth a little oblique.

Sculpture of 30-35 radial ribs; rib sculpture discrepant, RV with a few anterior ribs with very weak nodules or ridges, LV with all but posterior area ribs distinctly but not strongly nodulose.

Periostracum a thin coating, rust to olivaceous brown in colour except for interspaces which bear umbonally directed rigid spicate bristles.

Shell white.

Adductors scars subequal. The posterior a little larger. Inner margin deeply crenulate.

SELECTED SHELL MEASUREMENTS : See figure 44.



FIG. 44-45. — 44 : Box plots of the ratios of Total Shell Length to Heigth (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of Anadara corbuloides (n = 12). 45 : Bar chart of Rib Number for 12 shells of Anadara corbuloides.

DISTRIBUTION : This species ranges throughout the Mediterranean and from Spain (Cadiz, HIDALGO, 1916) along the West African coast and south to northern Angola (Luanda), but is nowhere common.

MATERIAL EXAMINED : Algeria : No precise locality, 1 spm., leg. JOLY, 1921, MNHN. Tunisia : Gulf of Gabes, N. of Djerba, beach, 1 v., leg. BOUCHET and WARÉN, 1982, MNHN. Italy : Viaregio, 2 spm., coll. DEL PRÊTE, MNHN. Mauritania : 17°42' N/16°16' W, 54 m, 1 spm., dredged R/V "N'Diago", leg. RICHER

DE FORGES, 1981, MNHN. Senegal : Kayar, north of Dakar, 110-120 m, 1 v., leg. MARCHE-MARCHAD, 6.IV.1967; 14°30,6' N/17°18,9' W, 43 m, 1 v., leg. LEUNG TACK, 1983-1984, both MNHN. Liberia : 4°34,5' N/8°31' W, 64 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. Côte d'Ivoire : Off Abidjan, 1 v., leg. MARCHE-MARCHAD, MNHN. Ghana : 4°40' N/2°08' W, 50 m, 1 spm., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. Cameroon : Between Wouri estuary and Cap Nachtigal, 3°43' N/9°13' E, 32-35 m, 1 v., trawled "Campo Star", leg. von CoseL, 22-29.XI.1985, 2°23' N/9°41' E, 45 m, 1 v., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, both MNHN. Angola : Off Ponta das Lagostas, Bengo, province, 30-50 m, 2 spm., leg. GoFAS, MNHN.



MAP 13. — Distribution of Anadara corbuloides.

BIOTOPE : Anadara corbuloides lives in fine muddy sand or mud, well offshore from 30 m to 60 m and occasionally deeper.

REMARKS : Anadara corbuloides apparently has two counterparts in the Panamic Pacific province, namely A. mazatlanica (Hertlein and Strong, 1943) and Scapharca (Caloosarca) biangulata (Sowerby, 1833). The fact that these species are placed in different genera by KEEN (1971) shows how the use of the equivalve condition gives rise to anomalous supraspecific classification. In A. corbuloides the juveniles are distinctly inequivalve but this condition becomes obsolete with ontogeny.



FIG. 46. — Internal view of right valve and dorsal view of *Anadara corbuloides* (Monterosato). Angola. (Scale bar = 10 mm.)

## Genus SENILIA Gray, 1842

TYPE SPECIES : Arca senilis Linné, 1758 (SD Gray, 1847).

Senilia senilis (Linné, 1758) (Pl. VIII, 1A-B, 2, 3; fig. 49; map 13)

Arca senilis Linné, 1758 : 694.

TYPE MATERIAL : One specimen in the Linnean collection, London (Dodge, 1952 : 151).

TYPE LOCALITY: "Jamaica" (10th edition) but later emended to "O. Africano" (12th edition).

DESCRIPTION

Shell to 135mm in length. Equivalve at all sizes. Inflated about the umbos but wedge shaped in cross section; moderately to strongly umbonate. Inequilateral, beaks in the anterior third, strongly prosogyre.

Outline subrhomboidal-trigonal, anteriorly expanded, posteriorly to some degree attenuate. Posterior area not defined; posterior angle weak; posterior margin oblique, slope variable from 30° to 65°. Median area rather flat, never sulcate even in post larval sizes; ventral margin more or less straight, posterior ventral junction subacute to attenuate. Anterior margin broadly rounded. Dorsal margin relatively short, straight.

Dorsal area short, more or less flat to cleft, rhomboidal with anterior area much more broad. Ligament initially opisthodetic, developing beyond the beaks 20 mm and secondarily amphidetic in large or old shells; chevrons strong, numbering up to 8.

— 356 —

Hinge plate becoming massive, teeth in two series, separated by a narrow oblique gap; anterior set up to 15 teeth, posterior set up to 16 teeth. Teeth long weakly chevron shaped but often becoming divided or distorted, mostly more or less vertical.

Sculpture of 13-15 broad flattened smooth ribs, occasionally narrowed and more rounded especially in the least attenuate shells.

Periostracum persistent, a thin coating with very fine concentric thickenings in the interspaces. Colour initially olivaceous then reddish brown to black.

Shell white.

Adductor scars subequal. Inner margin with large crenulations.



FIG. 47-48. — 47 : Box plots of the ratios of Total Shell Length to Height (L/H), Tumidity (L/T) and Anterior to Beak Length (L/A-Bk) of *Senilia senilis* (n 21). 48 : Bar chart of Rib Number for 21 shells of *Senilia senilis*.

SELECTED SHELL MEASUREMENTS : See figure 47.

DISTRIBUTION : This species ranges from West Sahara (Rio de Oro) south to Angola.

MATERIAL EXAMINED : Mauritania : Port Étienne (now Nouadhibou) to Nouakchott, many v., from 12 sta., all subfossil, Miss. GRUVEL, 1908, MNHN. Senegal : Dakar, Marigot de Hann, 2 sp., 1 v., Miss. GRUVEL, V.1908; Sine-Saloun region, mangroves, 8 spm., leg. BOUCHET, 9.VIII.1973; S-Casamance : Katakalous Bôlon, muddy sand, 3-4 m, many juv. spm.; Ourong Bôlon, on sandbank, low tide, 1 spm.,



MAP 14. - Distribution of Senilia senilis. The empty circles indicates records of valves with subfossil appearance.

1 v.; Karabane, sandbank, 2 sh., all leg. VON COSEL, III.1988; all MNHN. Gambia : 1 sp., coll. D'AUGUSTIN, 1835, MNHN. Sierra Leone : Sierra Leone River, 1 spm., leg. LONGHURST, 13.X.1954, MNHN. Liberia : Cap des Palmes, 2 sh., old coll., MNHN. Côte d'Ivoire : Azuretti Lagoon, Grand Bassam, 1 v., leg. AUBERT DE LA RUE, 1950, MNHN. Ghana : Accra, on beach, 3 v., Miss. GRUVEL, 26.I.1910, MNHN. Benin : Icheppê-Olokun, 3 v.; Lac Abénué, 1 sh., both Miss. GRUVEL, 1910, MNHN. São Tomé : Off Punta Oquedelrey, 5 m, 3 sh., 3 v., all juv., dredged R/V "Calypso", leg. MARCHE-MARCHAD, 1956, MNHN. Cameroon : Victoria/Limbe, on beach, 6 sh., leg. VON COSEL, XII.1985, MNHN. Gabon : Baie de Cap Lopez, 3 sh., Miss. GRUVEL, 1910, MNHN. R.P. Congo : Cocobeach, 1 sh., coll. SOYER, 1969; Loango, 6 sh., Office Pointe-Noire, 1969; Pointe-Noire, Plage Mondaine, on beach, 1 v., leg. VON COSEL, XII.1985, all MNHN. Zaïre : Crique de Moanda, 1 sh., leg. Miss. GRUVEL, 1910, MNHN. Angola : Cabinda, 1 sh., leg. C. R. BOETTGER, 1909; Ponta do Mussulo, Luanda province, on beach, many sh.; Baia dos Tigres, Moçâmedes province, 1 sh., both leg. GOFAS, 1981-1985, all MNHN.

BIOTOPE : Senilia senilis is a typical marine-estuarine species with lives in sandy mud, fine muddy sand or fine sand in estuaries, lagoons and creeks with regular tidal and seasonal salinity changes, often in the vicinity of mangroves, where it may be found in great quantities. It tolerates reduced salinity as well hyper salinity and lives predominantly in the lower intertidal zone.

REMARKS : This species is quite variable in outline with some shells distinctly attenuate posteriorly and others rather shortened. In the latter this compression results in the ribs being narrower, more rounded and more elevated (pl. VIII, 3). The functional morphology of this species was discussed by YONGE (1955) and the recent and fossil ecology by DEBENAY and SY (1989).



FIG. 49. — Internal view of right valve and dorsal view of Senilia senilis (L.). Angola. (Scale bar = 5 mm.)

## Genus BATHYARCA Kobelt, 1891

TYPE SPECIES : Arca pectunculoides Scacchi, 1834 (OD).

DIAGNOSIS: The genus *Bathyarca* is placed in the Anadarine by NEWELL (*in* MOORE, 1969), but, as shown by OLIVER and ALLEN (1980), the genus contains both epibyssate and endobyssate species thus encompassing the range of morphology exhibited by both the Arcinae eg. *Barbatia* and the Anadarinae eg. *Scapharca*, The unique feature of the genus is the mantle extension which is present to some degree regardless of shell shape. This is one of the few examples in the Arcidae where a group of species can be isolated by a synapomorphy and consequently it is a more rigid group than either the Arcinae or Anadarinae. There may therefore be a case for raising the genus to subfamily level and creating genera to separate the epibyssate species from the endobyssate species (OLIVER, in prep.).

# Bathyarca grenophia (Risso, 1826) (Pl. VII, 4; fig. 50)

Arca grenophia Risso, 1826 : 313. Arca pectunculoides Scacchi, 1834 : 82.

TYPE MATERIAL : Holotype (1 valve) of A. grenophia in MNHN Paris; type material of A. pectunculoides not located.

TYPE LOCALITY : Not cited; here selected Nice, Mediterranean France.

DESCRIPTION

Shell to 6 mm in length. Inequivalve, RV fitting into LV, not greatly inflated. Inequilateral, beaks in the anterior half.

Outline suboval, posteriorly expanded. Posterior area indistinct, posterior angle rapidly becoming obsolete, posterior margin broadly rounded. Median area flattening or weakly

sinuate, ventral margin rounded, usually with an indentation at the byssal exit. Anterior margin rounded but distinctly narrower than posterior. Dorsal margin straight.

Dorsal area narrow, umbonal separation weak. Ligament of few chevrons restricted to behind the beaks.

Hinge plate weak, teeth in two series separated by a distinctly edentulous space, anterior set up to 5 teeth, posterior set up to 8 teeth. Teeth small, straight, lateral teeth becoming strongly oblique.

Sculpture weak, subcancellate. Periostracum weakly haired. Shell white.

DISTRIBUTION : Throughout the Atlantic and in the subarctic from Norway to Angola in the east and from Greenland to Bermuda in the west.

MATERIAL EXAMINED : **Ibero-Maroccan Gulf** :  $36^{\circ}46' N/07^{\circ}07' W$ , 368-371 m, 5 spm. + 2 v.;  $36^{\circ}36' N/07^{\circ}24' W$ , 478-491 m, 1 spm.;  $36^{\circ}15' N/08^{\circ}01' W$ , 1340-1263 m, 15 spm.;  $35^{\circ}54' N/06^{\circ}13' W$ , 133-137 m, 1 v.;  $35^{\circ}54' N/06^{\circ}14' W$ , 150 m, 3 spm.;  $36^{\circ}41' N/07^{\circ}19' W$ , 543-544 m, 4 spm.;  $35^{\circ}54' N/06^{\circ}14' W$ , 293 m, 6 spm.;  $35^{\circ}35' N/03^{\circ}45' W$ , 480 m, 5 spm.;  $35^{\circ}31' N/07^{\circ}26' W$ , 1209-1302 m, 2 spm.;  $35^{\circ}26' N/04^{\circ}19' W$ , 170 m, 1 spm.;  $34^{\circ}24' N/07^{\circ}31' W$ , 1203 m, 1 spm.;  $34^{\circ}21' N/07^{\circ}24' W$ , 885-895 m, 6 spm.;  $33^{\circ}49' N/08^{\circ}24' W$ , 255-267 m, 5 spm.;  $33^{\circ}46' N/08^{\circ}30' W$ , 309 m, many spm.;  $33^{\circ}45' N/08^{\circ}32' W$ , 345 m, 1 spm., 6.VI.2984, all dredged R/V "Cryos", BALGIM campaign, all MNHN. Senegal :  $230^{\circ}$  off Cap Manuel, 120-215 m, many v. + 1 sh., in stomach of holothurian; off Dakar,  $14^{\circ}27' N/17^{\circ}33' W$ , 150-250 m, many v.;  $14^{\circ}53' N/17^{\circ}30' W$ , 205-230 m, 1 spm. + 3 v.; 170-200 m, 3 spm. + <math>19 v.; Baie de Gorée, 80-250 m, 14 v.; SW of Gorée, 150-250 m, 5 v., all dredged "Gérard Tréca", leg. MARCHE-MARCHAD, 1954-1958; all MNHN. Also based on the material used by OLIVER and ALLEN (1980).

BIOTOPE : This species lives attached to hard substrates and secondary hard substrates in soft sediment areas such as small stones, dead shells, worm tubes etc. In the north of its range it is found in the sublittoral zone as shallow as 2 m but further south it submerges to become a bathyal species and off the west African coast is found from 100-1300 m.

REMARKS : Comparing the west African material and more typically that from the greater end of the depth range with the northern shallow water material it is noted that the former possesses a thinner almost translucent shell in which the sculpture is very weakly developed. In these respect it resembles the form *pellucida* described by OLIVER and ALLEN (1980) from similar depths off the eastern American coast. Also amongst the BALGIM material from the Ibero-Maroccan gulf are many specimens of *Bathyarca obliqua* Philippi. This species is larger and more elongate than *B. grenophia* with a resultantly longer hinge line. It also ranges further north to boreal waters but as yet it has not been recorded from the west African coasts south of Morocco.

> Bathyarca inaequisculpta (Smith, 1885) (Pl. VIII, 5; fig. 51)

Arca (Scapharca) inaequisculpta Smith, 1885 : 267, pl. 17, figs. 8a-d. Bathyarca dakarensis Locard, 1898 : 321, pl. 8, figs. 25-28.

TYPE MATERIAL : Syntypes in BMNH. The syntypes of B. dakarensis are in MNHN.

TYPE LOCALITY : Off Culebra Islands, West Indies. The type locality of *B. dakarensis* is off Dakar, Senegal.



FIG. 50-51. — 50: Internal view of left valve of *Bathyarca grenophia* (Risso). Senegal, 150-250 m. 51: Internal view of right valve and dorsal view of *Bathyarca inaequisculpta* (Smith). Angola, 3797 m. (Scales bars = 1 mm.)

## DESCRIPTION

Shell to 8 mm in length. Inequivalve. Inflated. Inequilateral, beaks in the anterior half. Outline subcircular, as high or higher than long. Posterior area and posterior angle not demarcated. Margins other than dorsal not differentiated, round. Dorsal margin relatively long and straight. Median area curved, not sulcate.

Dorsal area narrow, umbonal separation slight. Ligament with few chevrons restricted to behind the beaks.

Hinge plate narrow, teeth in two series but separation obscure, anterior set up to 8 teeth, posterior set up to 10 teeth. Teeth small, straight, lateral teeth becoming strongly oblique.

Sculpture weak, finely decussate, often a little stronger RV. Periostracum weak, sparsely pilose. Shell white.

DISTRIBUTION : This species is widely distributed in bathyal and abyssal zones throughout the Atlantic Ocean from 50 N to  $14^{\circ} \text{ S}$ .

MATERIAL EXAMINED : The material examined is that used by OLIVER and ALLEN (1980).

BIOTOPE : This is a truly deep sea species and is confined to abyssal oozes in which it lives at or near the surface anchored to sediment particles by a multi threaded byssus. Although it has been found as shallow as 700 m it is more typically abyssal ranging from 1900-5000 m.

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#### PLATE I

- 1A-D. -- Arca noae Linné : West Sahara, off Cap Barbas, 21°05'N/17°14'W, 43-45m, MNHN. 73mm. 1A, periostracum removed.
- 2. Arca noae Linné : Cape Verde Islands, Ilha do Sal, Santa Maria, on beach, MNHN. 11.5 mm.
- 3A-D. Arca bouvieri Fischer : Angola, Cacuaco, Bengo province, 5-10 m, MNHN. 60 mm. 3A, periostracum removed.
- 4. Arca bouvieri Fischer : Angola, Corimba, Luanda province, 10-20 m, MNHN. 11 mm.


PLATE I

# PLATE II

- 1A-D. Arca avellana turbatrix n. ssp. : Holotype. Angola, Santo Antonio, Benguela province, intertidal, rocks. MNHN. 31mm. 1A, periostracum removed.
- MNHN. 31 mm. 1A, penostracum removed.
  2. Arca avellana turbatrix n. ssp. : Paratype. Angola, Lucira, Moçâmedes province, MNHN. 18.7 mm.
  3A-B. Arca imbricata Bruguière : Florida, NMWZ. 50 mm. 3A, periostracum removed.
  4. Arca avellana Lamarck : Seychelles, MNHN. 30 mm, periostracum removed.
  5A-B. Arca tetragona Poli : Ireland, Berehaven, Bantry Bay, NMWZ. 21.3 mm.
  6. Arca tetragona Poli : England, Falmouth, NMWZ. 26.6 mm.

- 7A-B. Acar plicata (Dillwyn) : Cape Verde Islands, Mindelo, São Vicente, MNHN. 7A, 19.1 mm; 7B, 18.2 mm. 8A-B. Acar pulchella (Reeve) : Mediterranean, Algeria, MNHN. 18.2 mm.



PLATE II

# PLATE III

- 1A-B. Barbatia complanata (Bruguière) : Côte d'Ivoire, Canal de Vridi, Abidjan, MNHN. 1A, 51 mm; 1B, 18 mm.
- 2. Barbatia complanata (Bruguière) : Angola, Chapeu Armado, Moçâmedes province, rocks at low tide, MNHN. 40 mm.
- 3. Barbatia complanata (Bruguière) : Angola, Caotinha, Benguela province, MNHN. 33 mm.
- 4. Barbatia complanata (Bruguière) : Angola, Lucira (Praia do Cesar), Mocâmedes province, MNHN, 45 mm. 5A-B. — Barbatia complanata (Bruguière) : Angola, Praia Amelia, Moçâmedes province, rocks at low tide, MNHN.
- 5A, 22 mm; 5B, 16 mm.
- 6A-B. Barbatia gabonensis n. sp. : Holotype. Gabon : off Mayumba, 3°25' S/9°56' E, 100 m, MNHN. 27.7 mm. 7A-B. Barbatia ionthados n. sp. : Holotype. Côte d'Ivoire, Sud Bassam, 200 m, MNHN, 20.6 mm. 8. — Barbatia legumen (Lamy) : Angola, Corimba, Luanda province, Praia Etambar, between rocks at low tide,
- MNHN. 41 mm.
- 9A-B. Barbatia legumen (Lamy) : Angola, 10 km. S of Ambrizete, Zaire province, intertidal, on beach, MNHN. 24 mm.
- 10. Barbatia legumen (Lamy) : R.P. Congo, Pointe-Noire, Plage Mondaine, MNHN. 53 mm.



PLATE III

## PLATE IV

- 1A-B. Barbatia (Nipponarca) allocostata n. sp. : Holotype, Guinea-Bissau : Mouth of Rio Geba, 11°57,5' N/ 16°27' W, 7m, MNHN. 27.7mm.
- 2. Barbatia (Nipponarca) allocostata n. sp. : Paratype as holotype, MNHN, 28 mm, periostracum removed.

3A-B. — Anadara geissei (Dunker) : Angola, Baie de Corimba, Luanda province, 10-20 m, MNHN. 71 mm. 4A-B. — Anadara geissei (Dunker) : Angola, Cacuaco, Bengo province, 5-10 m, MNHN. 4A, 33 mm; 4B, 18 mm. 5. — Anacara geissei (Dunker) : Guinea, 9°50' N/14°14' W, 15m, MNHN. 52mm.

6A-B. — Anadara geissei (Dunker) : Cape Verde Islands, São Vicente, Baia Porto Grande, on beach, MNHN. 6A, 50 mm; 6B, 48 mm.



PLATE IV

### PLATE V

- 1A-B. Anadara polii (Mayer) : Mediterranean, Banyuls, MNHN. 34mm, oblong morph.
- Anadara polii (Mayer) : Mediterranean, Naples, MNHN. 39 mm, intermediate form.
   3A-C. Anadara polii (Mayer) : Atlantic Morocco, MNHN. 3A, 30°24' N/09°54' W, 105 m, 28 mm, oblong morph. 3B, 30°26' N/09°44' W, 65 m, 23 mm, anteriorly constricted morph. 3C, 30°05' N/09°50' W, 110 m, 22 mm, globose morph.
- 4A-B. Anadara polii (Mayer) : Senegal, 14°50,1' N/17°29,3' W, 150 m, MNHN. 4A, 31 mm, oblong morph. 4B, 29 mm, globose morph.
- 5. Anadara polii (Mayer) : Côte d'Ivoire, 05°01' N/05 °17' W, 40 m, MNHN. 24 mm, oblong morph.

- Anadara polii (Mayer): Côte d'Ivoire, off Abidjan, 70m, MNHN. 22mm, oblong morph.
   Anadara polii (Mayer): Côte d'Ivoire, off Abidjan, 70m, MNHN. 22mm, oblong morph.
   Anadara polii (Mayer): Senegal, off Dakar, 200m, MNHN. 24mm, anteriorly constricted morph.
   Anadara polii (Mayer): Cameroon, 02°39' N/09°40' E, 60-65 m, MNHN. 26 mm, anteriorly constricted morph.
   Anadari polii (Mayer): Gabon, 00°32,8' N/08°43,1' E, 125-145 m, MNHN. 39 mm, anteriorly constricted morph.



PLATE V

## PLATE VI

— 374 —

- 1A-D. Anadara eborensis n. sp. : Holotype. Côte d'Ivoire, off Grand Bassam, 20 m, MNHN. 31.9 mm.
- 2A-B. Anadara subglobosa (Dunker) : Mauritania, 17°30' N/16°15' W, 100 m, MNHN. 18.5 mm.
  3A-D. Anadara senegalensis (Gmelin) : Côte d'Ivoire, off Abidjan, 20 m, MNHN. 18.5 mm.
  3A-B. Anadara senegalensis (Gmelin) : Côte d'Ivoire, off Abidjan, 20 m, MNHN. 3A-C, 21.8 mm. 3D, 23.5 mm.
  4A-B. Anadara senegalensis (Gmelin) : Guinea-Bissau, 12°05' N/17°02,5' W, 14 m, MNHN. 21.8 mm.
  5A-B. Anadara senegalensis (Gmelin) : Angola, Cacuaco, Bengo province, 0-10 m, MNHN. 15.8 mm.
  4A-B. Anadara senegalensis (Gmelin) : Angola, Cacuaco, Bengo province, 0-10 m, MNHN. 15.8 mm.

- 6A-C. Anadara camerunensis n. sp. : Holotype. Cameroon, Victoria/Limbe, 8-10 m, MNHN. 15.1 mm.



PLATE VI

# PLATE VII

- 1. Anadara senegalensis (Gmclin) : Senegal, South Casamance, Cap Skirring-Diembéring, on bcach, MNHN. 23.1 mm.
- 2. Anadara senegalensis (Gmelin) : Senegal, South Casamance, Cap Skirring-Diembéring, on bcach, MNHN. 25.4 mm, Casamance variant.
- 3. Anadara senegalensis (Gmelin) : Senegal, North Casamance, Abéné-Kafoutine, on beach, MNHN. 23.0 mm, intermediate form.
- 4. Anadara senegalensis (Gmelin) : Senegal, North Casamance, Abéné-Kafoutine, on beach, MNHN. 26.2 mm, Casamance variant.
- 5A-D. Anadara corbuloides (Monts.) : Angola, off Ponta das Lagostas, Bengo province. 30-50 m, MNHN. 69 mm.



PLATE VII

## PLATE VIII

- 1A-B. Senilia senilis (Linné) : Angola, Cacuaco, Bengo province, MNHN. 92 mm.
- 1A-D. Senuta senuts (Linne) : Angola, Cacuaco, Bengo province, MINHN. 92 mm.
  2. Senilia senilis (Linné) : Angola, Pta. do Mussulo, Luanda province, MNHN. 50 mm.
  3. Senilia senilis (Linné) : Gabon, Cap Esterias, Pointe Idolo, MNHN. 39 mm.
  4. Bathyarca grenophia (Risso) : Morocco, 35°35′ N/03°45′ W, 480 m, MNHN. 8.4 mm.
  5. Bathyarca inaequisculpta (Smith) : Angola, 14°40′ S/09°54′ E, 3797 m, NMWZ. 6.7 mm.
  6A-B. Bentharca asperula (Dall) : Angola, 14°31,8′ S/09°46′ E, 3975 m, NMWZ. 10.7 mm.



PLATE VIII

# PLATE IX

Scanning electron micrographs of the periostracal bristles from the carinal ridge of : A, Arca avellana turbatrix n. ssp. and B, Arca imbricata (Brug.) from Florida. (Scale bar = 0.5 mm.)



PLATE IX